Sebastes

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An Historical Review of *Sebastes* Taxonomy and Systematics

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Discovery: The Late 1700's

The systematics of the speciose genus *Sebastes*[1], rockfishes, particularly in the North Pacific, have challenged ichthyologists and others even casually in-

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[1] *Sebastiscus* and *Hozukius* have been considered subgenera of *Sebastes* by some and separate but closely related genera by others. This paper will consider each a separate genus and will focus primarily on the taxonomic history of *Sebastes*. *Sebastes* is by far the most species-rich and widely distributed genus; *Sebastiscus* and *Hozukius* have three and two species, respectively, and occur only in the northwest Pacific. As will be discussed later, *Sebastes* and these other two genera form an unresolved trichotomy within the Sebastidae of the suborder Scorpaenoidei (Ishida, 1994). These three genera could be given the subfamily name Sebastinae, following Matsubara (1943).

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ABSTRACT—Following the initial description of a species of Sebastes *from the Atlantic in the late 1700's, in the late 1800's the incredible taxonomic diversity of the genus began to be recognized as more species were discovered in northeast Pacific waters. With over 100 species, most of them from the North Pacific, the genus* Sebastes *(rockfishes) now presents taxonomic problems at every level. For example, although early efforts to understand relationships among the species resulted in the erection of several subgenera, those and more recent efforts remain largely unsuccessful. Also, the position of the genus within the order Scorpaeniformes, as well as the limits of the genus and the validity of some species are all unresolved. This paper examines the worldwide history and status of taxonomic studies on* Sebastes, *and reviews the 23 subgenera that have been erected over the years. This review of research, which includes morphological and genetic studies, provides a framework against which to evaluate studies using new genetic techniques.*

terested in these fishes for well over a century. Fernholm and Wheeler (1983) detailed problems associated with the early descriptions of *Sebastes*. The first scholarly reference to a rockfish was by Linnaeus (1761) who included Norway and Italy as the range of a fish he described in 1758 and named *Perca marina*. In his former publication (Linnaeus, 1758), he also described *Perca scriba*, a Mediterranean serranid. Reiterating his description of *Perca marina*, Linnaeus (1761) cited the common Norwegian name (uer or rödfisk) for the fish from Norway, making it clear that he was including a rockfish, as well as a fish from the Mediterranean region in his description.

Cuvier (1829) was the first to use the generic name *Sebastes*, and in his second, and much more thorough description of the genus (Cuvier and Valenciennes, 1829) he included descriptions of species from the North Atlantic (*Sebastes norvegicus*), the Mediterranean Sea (*S. imperialis = Helicolenus dactylopterus*), and the Southern Hemisphere (*S. capensis*).[2] Cuvier and Valenciennes (1829) recognized the confusion between the northern fish and *Perca marina*, which he said was "hardly believable"; nevertheless, the name *Sebastes marinus* (Linnaeus) was used until recently for this fish from the North Atlantic. However, Fernholm and Wheeler (1983) found that the specimen Linnaeus used as the basis of his description was in fact the Mediterranean serranid *Serranus scriba*, so *Sebastes (Perca) marina* became a syn-

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[2] See Simpson, A. J., A. W. Kendall, Jr., and J. W. Orr. 2000. Translations of the original descriptions of *Sebastes* by Georges Cuvier. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle WA 98115. Proc. Rep. 2000-09, 24 p.

onym of *Serranus scriba*, and the rockfish was left without a type species for reference. This made way for recognizing Ascanius (1772) as the author of *Perca norvegica* (i.e. *Sebastes norvegicus*), the most common rockfish of the northeastern Atlantic.

Proliferation of Subgenera: 1861–1898

By 1845, similar fish had been described as species of *Sebastes* from both the eastern and western North Pacific. In 1854, Ayres discovered *Sebastes paucispinis* from off California (Ayres, 1854a). Since *Sebastes paucispinis* is very different from *Sebastes norvegicus*, but clearly related to it, its discovery prompted Gill (1861) to erect another genus for it: *Sebastodes*. This began a trend by Gill and others to establish generic or subgeneric groupings as more and more similar species were described on both sides of the North Pacific during the 1860's–1880's (Fig. 1, 2). By 1898, Jordan and Evermann grouped the 55 northeast Pacific species that they recognized into 13 subgenera (Jordan and Evermann, 1898). They also mentioned 13 species from Japan and 3 species from the Southern Hemisphere. Generally the characters of a proposed subgenus were only those of the type species for the subgenus. In most cases the definitions of the subgenera were inferred rather than explicitly stated (Appendix I).

Confusion: 1863–1900

There was considerable disagreement among ichthyologists of the late 1800's concerning these subgenera of northeast Pacific rockfishes and the importance of the characters used to distinguish them. Reading the papers of Ayres (1854a, b, 1855, 1859, 1863a, b, c, d), Gill (1861,

North Atlantic
Sebastes
(Cuvier, 1829)

Northwest Pacific
Sebastes
(Cuvier, 1829)

Northeast Pacific

1860

Sebastes
(Ayres, 1854-1863d)

Sebastodes

Sebastichthys
(Gill, 1862a)

Sebastodes **Sebastichthys** **Sebastomus** **Sebastosomus**
(Gill, 1864)

Sebastodes **Sebastichthys** (with subgenera)
(Jordan and Gilbert, 1880)

(Hilgendorf, 1880)

1880

Sebastodes
(Jordan and Gilbert, 1883)

(Steindachner and Döderlein, 1884)

Sebastodes **Sebastichthys**
(Jordan, 1887)

Sebastodes *Sebastichthys* *Sebastomus* *Sebastosomus*
Acutomentum *Auctospina* *Primospina* *Pteropodus*
(Eigenmann and Beeson, 1893)

Sebastodes
(Cramer, 1895)

Sebastodes (with 13 subgenera)
(Jordan and Evermann, 1896, 1898)

Sebastodes
(Jordan and Evermann, 1898)

1900

Sebastodes **Sebastichthys**
(Jordan and Starks, 1904)

Emmelas **Sebastodes** **Sebastosomus**
Primospina *Acutomentum* *Sebastomus*
Sebastocarus *Sebastopyr* *Rosicola*
Hispaniscus *Auctospina* *Pteropodus*
Sebastichthys *Eosebastes* *Zalopyr*

Sebastes (with 10 subgenera)
(Jordan and Hubbs, 1925)

(Jordan et al., 1930)

Sebastes (with 10 subgenera)
(Matsubara, 1943)

Sebastes
(Matsubara, 1943)

Figure 1.—Chronology of generic and subgeneric names for *Sebastes*. Based on Ishida (1984). Generic names are in bold. References below the names propose or support all the names on the line above them.

1862a, b, 1864), Jordan and Evermann (1896, 1898), Eigenmann and Beeson (1893, 1894), and Cramer (1895) on the subject indicates that more heat than light was generated. For example, by 1862 Gill had erected two genera (*Sebastodes* for *Sebastes paucispinis*, and *Sebastichthys* for all other species) for northeast Pacific rockfishes. He based these subgenera on a few morphological characters. Ayres (1863a, d) rejected the characters of Gill, but placed the 11 species known to him in two genera: one with smooth heads, for which he used the name *Sebastodes*, and the other with spiny heads, which he suggested be included with the North Atlantic species in *Sebastes*. In Gill's 1864 paper "Critical remarks on the genera *Sebastes* and *Sebastodes* of Ayres" he stated: "The value of the characters used to distinguish the genera *Sebastes*, *Sebastichthys* and *Sebastodes* are now indeed so generally conceded by scientific men, that it is unnecessary to further argue in their favor. I shall only remark that the combinations and distinction of forms by Dr. Ayres are alike unnatural and violate all natural affinities . . ." In discussing Ayres' ideas on affinities of flatfishes, Gill (1864) stated: "Dr. Ayres . . . ideas of affinity are extremely crude and unreliable, nothing can be learned from them." However, in discussing this paper Günther (1865) commented: "Dr. Gill would advance ichthyology by giving us serviceable descriptions, in-
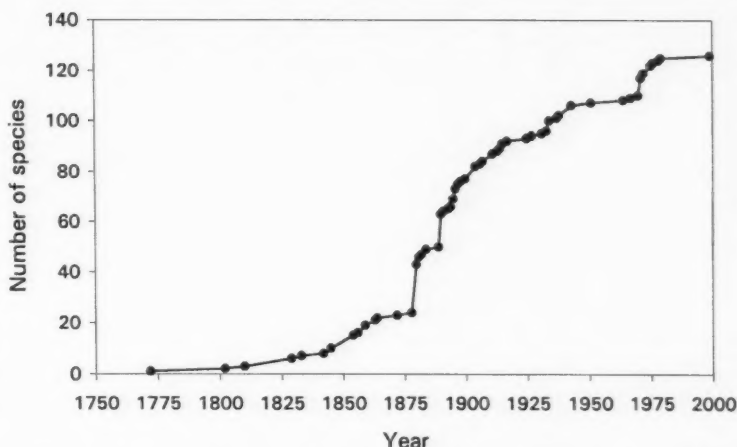

Figure 2.—Cumulative number of described and currently recognized species of *Sebastes*.

stead of limiting himself to synoptical tables with minute sub-generic subdivisions. As regards his frequent critical remarks on synonyms, it would be very useful if he would state whether he arrived at his conclusions from an examination of typical specimens, but it is not even evident whether he has known the species from autopsy." Ayres (Fig. 3) was not the only naturalist from San Francisco to receive severe criticism from Gill (Fig. 4): "Of course, Gill had an agenda for this criticism for he objected to the intrusion of these Californian upstarts, amateurs in his opinion, in what he had carved out as his person-

al fiefdom, the fishes of the North Pacific" (Leviton and Aldrich, 1997, footnote 16.3, p. 196).

In 1880, Jordan and Gilbert (1880) described 7 new species from California, and after trying to place them in the four genera then recognized by Gill, they left *paucispinis* in *Sebastodes* and stated that: "the groups *Sebastosomus* and *Sebastomus* cannot be maintained as genera distinct from *Sebastichthys*, and that, in order to recognize them as subgenera even, a different distribution of species must be adopted."

Eigenmann and Beeson (1893, 1894) tried to bring some order to the argument
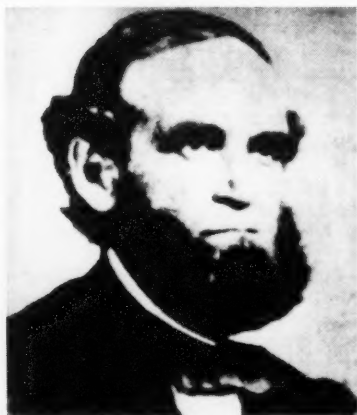
Figure 3.—Photograph of W. O. Ayres, reproduced through courtesy of California Academy of Sciences Archives. William Orville Ayres (1805–1887) was born in Connecticut and educated at Yale University to be a medical doctor (Hawkes, 1887). An early interest in natural history caught the attention, and fostered the friendship of J. J. Audubon, who named a woodpecker (*Picus ayresii*) in Ayres' honor stating "I have named this handsome bird after my young and learned friend W. O. Ayres, Esq. who is well known to science as an excellent ichthyologist; and who is well conversant with the birds of our country" (as seen in 1967 republication of Audubon, 1840–1844 [the bird is now considered a hybrid of the yellow- and red-shafted flicker]). In 1844, coincident with Audubon's death, convinced that "no field had been ungleaned in ornithology, [Ayres] turned to the water, teeming with attractive life and

pregnant with interest for him" (Hawkes, 1887). Ayres migrated to San Francisco in 1854 and became a leading member and officer in the California Academy of Sciences, which met every, or every-other Monday evening in the 1850–1870 period, to hear of new natural history discoveries of the area. Besides maintaining a highly-regarded medical practice, Ayres often presented descriptions of fishes he came across at the fish markets, and even presented information on birds at some of the meetings. However ". . . Gill's ruthless criticism of Ayres, finally caused Ayres to give up research in ichthyology in 1864. Ayres left San Francisco in 1871 and returned East, first to Chicago, Ill., where he suffered serious financial reversals and then in 1878 to New Haven, Conn., where he re-established his medical practice and taught at Yale's medical school" (Leviton and Aldrich, 1997: footnote 3.2, p. 43).

Figure 4.—Photograph of T. N. Gill, reproduced with permission (Neg. #SA602. Theodore N. Gill. Smithson-

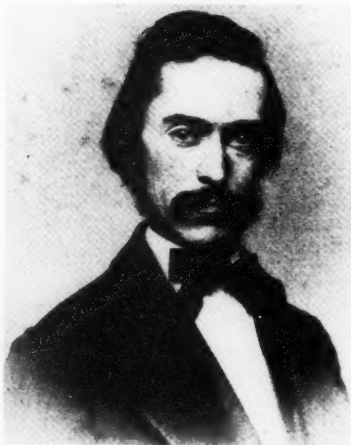ian Institution Archives. Record Unit 95, Photograph Collection, 1850s-). Theodore Nicholas Gill (1837–1914) grew up in New York City where early visits to the Fulton Fish Market spurred his interest in ichthyology (Dall, 1916). Early on Gill was schooled in the classical languages, with his father intending him to study theology, but this, as well as a job in a law firm, did not suit him, and his inclination in natural history prevailed. He was granted a scholarship to study science in Philadelphia, and from there he went to Washington, D.C., where he found a mentor and supporter in S. F. Baird at the Smithsonian Institution. Baird published one of Gill's first papers, on the fishes of New York, when Gill was only 19 years old (Gill, 1856). Shortly thereafter Gill made his only extensive field trip in which he studied the marine and freshwater fishes of the Antilles Islands. Upon returning to Washington he settled at the Smithsonian and, through Baird's influence, was appointed to work on fishes collected during the Northwest Boundary Survey.

During this work he encountered many of the newly described and undescribed species of *Sebastes* from the northeast Pacific and the work of W. O. Ayres on them. As a result of his studies he published several descriptions of new species and erected several new genera to contain Pacific *Sebastes*. In these publications he frequently questioned Ayres' work, and eventually published (Gill, 1864) a criticism of Ayres (Ayres, 1863a) who had taken Gill to task for his classification of rockfishes. Ayres took this criticism so hard that he ceased to publish ichthyological papers. Gill remained in Washington, D.C., for the rest of his life, working on fishes, mollusks, mammals, and birds. Gill's strength was in higher order classification rather than in species descriptions ("In matters of classification [taxonomy] he was easily first in the world" Jordan (1931)). He had a reputation of being very helpful to up-coming students of natural history, but this did not seem to extend to Ayres.

by publishing a key and diagram of relationships for the eight subgenera they recognized (with *mystinus* as the sole member of *Primospina* representing the base from which all other species radiate) (Fig. 5). However, a footnote by the editor (R. Edward Earll) to the title of the 1894 paper which appeared in the Proceedings of the U.S. National Museum stated: "The classification adopted by the authors of this paper is based on their own peculiar interpretation of the importance of certain structural characters. The arrangement and nomenclature proposed here will not be, at present at least, followed by the National Museum." Fur-

ther, Cramer (1895), in his detailed study of the cranial osteology of these fishes, took strong exception with the importance of the first dichotomy (union or nonunion of the parietals) in the key of Eigenmann and Beeson (1893). Since Cramer's work was in essence a rebuttal of the work of Eigenmann and Beeson, he included their entire article as an appendix to his paper. Cramer (1895) did not explicitly recognize any subgenera for the 32 species of *Sebastes* he examined, but his key to species based on cranial characters exactly groups the species into the subgenera eventually used by Jordan and Evermann (1898) in their

classic "The Fishes of North and Middle America." In the introduction to their species accounts of *Sebastes*, Jordan and Evermann (1898) included from Cramer (1895) extensive quotations from his text, and his entire key to species, which they amended slightly by adding a few species Cramer did not consider, and from Eigenmann and Beeson (1893) their key to subgenera. Jordan and Evermann (1898) commented on Eigenmann and Beeson's (1894) work saying: "Messrs. Eigenmann & Beeson have attempted to subdivide this genus into several subgenera on the basis of cranial characters. Mr. Cramer has given in detail...his reasons for rejecting these proposed genera and for reverting to the sequence of species in Jordan & Gilbert's Synopsis [1883]. The character especially put forward by Eigenmann & Beeson, that of the contact (not union) of the parietals, seems to us of very slight value, even at a specific distinction."

Consolidation: the Early 1900's

The proliferation of subgeneric names for rockfishes of the Northeast Pacific slowed after the turn of the 20th century. One more was proposed by Jordan and Hubbs (1925), two more by Jordan and Evermann (1927), and one by Hubbs (1951). Through the first half of the
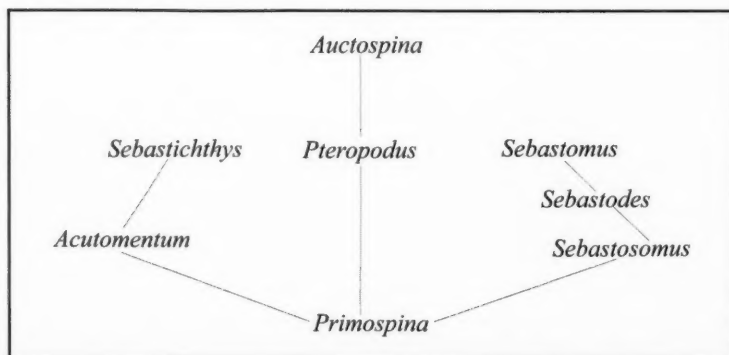

Figure 5.—Relationships among subgenera of *Sebastes* proposed by Eigenmann and Beeson (1893).

20th century, authors variously lumped, split, or ignored subgenera completely. Although in their "Checklist of Fishes of North and Middle America," Jordan et al. (1930) placed 66 species of rockfishes they recognized in 16 genera (that is, they elevated the subgeneric names to generic status), most American researchers used only two genera: *Sebastes* for Atlantic species and *Sebastodes* for Pacific species, disregarding the subgenera.

Matsubara (1943) (Fig. 6) presented a very detailed analysis of the Scorpaenidae of the Northwest Pacific. He subdivided the family into 14 subfamilies, and in the Sebastinae he included four genera, one of which was *Sebastes*. He grouped the 30 species of *Sebastes* he considered into 10 subgenera, 5 of which were newly erected. The five previously established subgenera he used had representative species in the Northeast Pacific also. Matsubara (1943) provided a key to the subgenera he used, and descriptions based on a number of osteological, meristic, and morphometric characters. He also concluded that there was no validity in grouping the Atlantic species of *Sebastes* separately from the Pacific species (then considered in *Sebastodes*), and since *Sebastes* is the older name it takes precedence.

The early-described Pacific species have fewer dorsal spines and vertebrae than the Atlantic species, characters thought important enough to justify placing the species from the two oceans in separate genera. However, species were later found in the northern Pacific Ocean and Bering Sea that have vertebral and dorsal spine counts approaching those of the Atlantic species, calling into question the rationale for maintaining the generic distinction. This change in thinking is reflected in successive editions of the American Fisheries Society's "List of Common and Scientific Names of Fishes from the United States and Canada." The first two editions (AFS, 1948; Bailey et al., 1960) recommended *Sebastes* for Atlantic species and *Sebastodes* for Pacific species; however, later editions (Bailey et al., 1970; Robbins et al., 1980; 1991) recommended using *Sebastes* for rockfish-

es from both the Atlantic and Pacific waters of North America.

## Limited Morphological Studies: the 1970's

Chen (1971) reviewed *Sebastomus*, the most distinctive subgenus of *Sebastes*. Occurring in the northeast Pacific and in the Southern Hemisphere, *Sebastomus* contains 16 species, which are all characterized by having strong head spines, the second anal spine longer than the third, and a series of six large white blotches (one at the tip of the opercle and five between the dorsal fin and lateral line [not all are present in all species]). Chen (1971) gave detailed accounts of the species and constructed a diagram of relationships among the 13 then-known species based on a subjective analysis of about 15 characters. He considered phenetic similarity among the species in constructing his diagram. The characters he used were color patterns, body configuration (morphometrics and head spines), and meristics. He did not specify the outgroup for his analysis, or what he considered to be the primitive states of the characters he used. Without this information and with the informal discussion of relationships he offered, it is difficult to evaluate his conclusions. Thus, even within this relatively well-known and cohesive species group, considerable additional work is needed.

Hallacher (1974) characterized the structure and points of attachment of swimbladder muscles for 82 species of *Sebastes*, and found two major types and seven patterns within these types. In general, he found little correspondence between species sharing the same muscle patterns and their placement in the proposed subgenera (including *Sebastomus*). For example, two similar appearing members of *Sebastodes* (*S. brevispinis* and *S. paucispinis*) had major differences in structure. However, all but one species of *Pteropodus* shared the same swimbladder muscle pattern.

During this period several new species were described or reviewed (e.g. Barsukov (1970), Chen (1975), Tsuyuki and Westrheim (1970)), and some studies dealt with the component species of some subgenera (e.g. the *Sebastes*

Figure 6.—Photograph of K. Matsubara, reproduced with permission of the American Society of Ichthyologists and Herpetologists. Kiyomatsu Matsubara (1907–1968) was a prominent ichthyologist and teacher of ichthyology in Japan, who credited his interest in fishes to Carl Hubbs (Hubbs, 1969). Matsubara published several papers on scorpaenoid fishes of Japan, capped by his seminal monograph revising the Japanese fishes in this suborder and providing significant insight into the systematics of the group worldwide (Matsubara, 1943). Considering the world situation at the time, besides the remarkable ichthyological endeavor this monograph represents, it is amazing that it was published in perfect English, in Tokyo. Although a species of *Sebastes* from Japan is named *S. matsubarae*, it was not named after this renowned ichthyologist; rather it was described by Hilgendorf in 1880, who named it after Shinnosuke Matsubara, director of the Imperial Fisheries Institute in Tokyo (Jordan and Starks, 1904). Besides his work on scorpaenoid fishes, Matsubara also published several more general volumes on systematic ichthyology and papers on various other fish groups of Japan. Although he worked at a time when limited access to foreign collections and literature forced many Japanese scientists to consider only local material in their work, Matsubara framed his work on scorpaenoids in a larger worldwide context. He was the first to suggest that the genera *Sebastes*, representing Atlantic species, and *Sebastodes*, representing Pacific species, be synonymized.
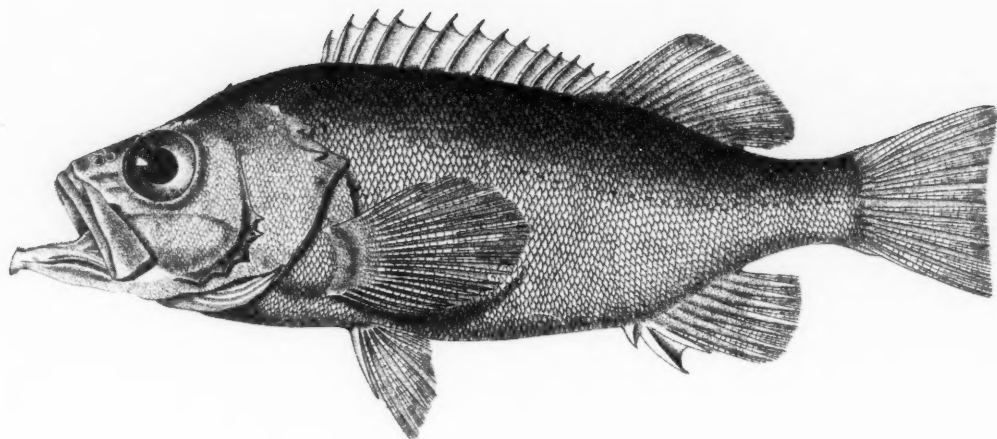
Sebastes norvegicus from Cuvier (1829): Plate 23, figure 3 (reproduced by permission of ASHER Rare Books, the Netherlands). This illustration accompanied the original description of the genus *Sebastes*.
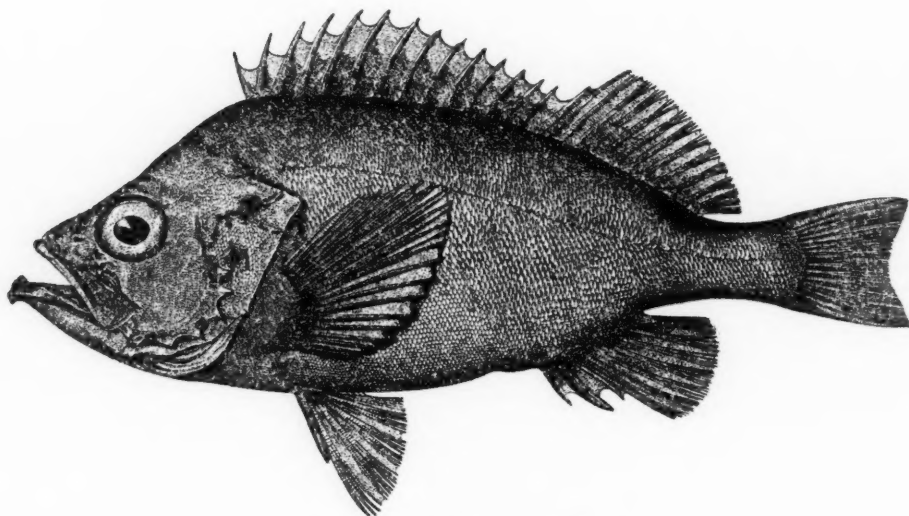
FIG. 141.—Rosefish (*Sebastes marinus*).

Sebastes marinus (probably *S. fasciatus*); drawn by H. L. Todd and originally published in Goode and Associates (1884). At the time of this publication only one species of *Sebastes* was recognized in the northwest Atlantic; however, three species are now known to occur there.

Memoir d. l'Acad. Imp. d. Sc. d. S. Petersb. Tom IV Tab. XVI.

Fig. 1

Fig. 4   Fig. 3   b   Fig. 2
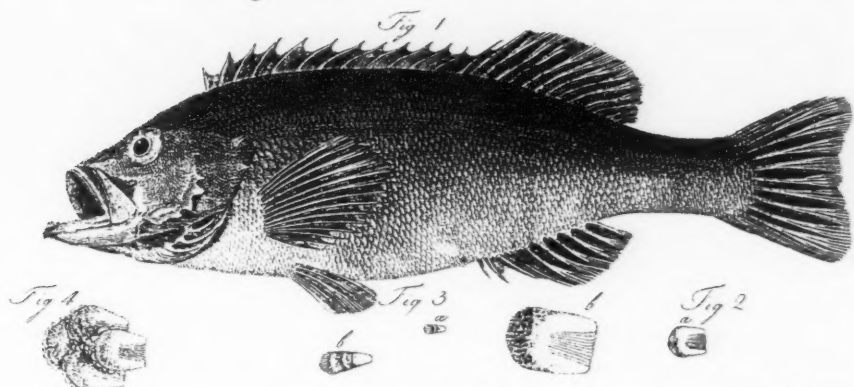
D.r Tilesius del.   *Epinephelus ciliatus*   F. Meyer sc.

Sebastes ciliatus from the original description of the species by Tilesius (1813). This was the first species of *Sebastes* to be described from the Northeast Pacific Ocean.
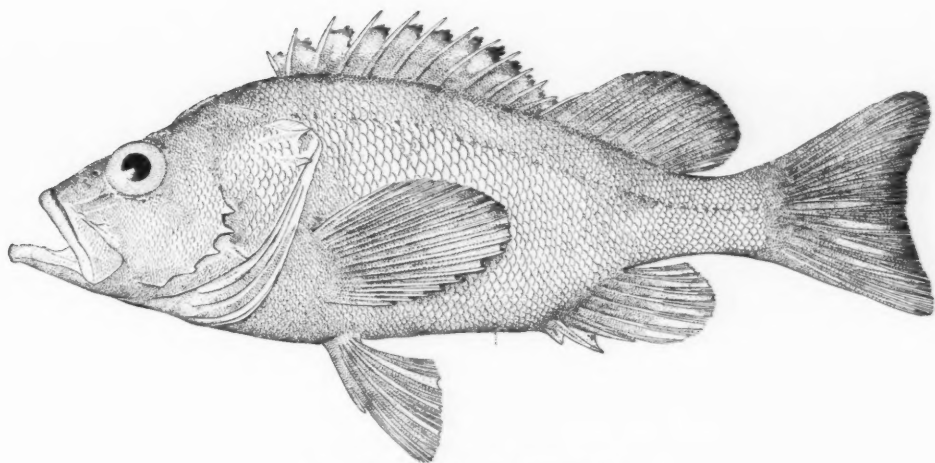
SEBASTODES ALEUTIANUS JORDAN & EVERMANN. TYPE.

Sebastes aleutianus from Evermann, and Goldsborough (1907). This is one of several fine illustrations of species of *Sebastes* from Alaska in this early publication.

vulpes "complex": Chen and Barsukov (1976), *Sebastiscus*: Barsukov and Chen (1978), and *Mebarus*: Chen (1985)).

Systematic morphological analysis of the entire genus during this period was limited to Barsukov (1981), who published a complex diagram of interspecific relationships of the Sebastinae based on a dubious speciation hypothesis (Kendall, 1991). Barsukov (1981) proposed that there were seven cycles in the evolutionary history of the Sebastinae. "In each one no more than three descendant species originated sympatrically from one ancestral species. Such a triad is characteristic of speciation with incomplete (mainly biotopic) isolation. A species, once established at intermediate depths, emerges into the extreme position of another dimension, i.e., it develops ecological and morphological features unique for the trio, and usually associated with adaptations to life in open water" (Barsukov, 1981:1). Based on this premise he reviewed the sequence of geological events that led to the divergence found in some lineages of these fishes, and related the morphology of living forms to their history, ecology, and zoogeography. For example, in the first cycle he considered the subfamily Sebastinae to be composed of three genera: the shallow water *Helicolenus* with 13 species, the intermediate depth *Sebastes* with 102 species, and the deep-water *Hozukius* with 2 species. In the second cycle he felt that the genus *Sebastes* split into three subgenera: the shallow water *Sebastiscus* with 3 species, the intermediate depth *Sebastodes* with 88 species, and the deep-water *Sebastes* with 14 species. More divergence occurred in the intermediate-depth branch than in the other two during each cycle, and some branching was not successful (incipient species became extinct). Using these questionable evolutionary principles Barsukov (1981) diagramed the relationships of all known species of the Sebastinae.

Genetics Enters the Picture: the Late 1900's

Starting in the 1960's, newly developed genetic techniques were applied to systematic studies of rockfishes. Bar-rett et al. (1966) examined electrophoretic patterns of hemoglobin in 27 species of *Sebastes* from off California and found that each species, including some morphologically similar species pairs (e.g. *Sebastes caurinus-S. vexillaris, S. eos-S. chlorostictus*), had a distinctive pattern. They also found shared patterns among species in some subgenera (e.g. *Pteropodus, Sebastomus*), but distinct differences among some members of other subgenera (e.g. *Sebastosomus*). This work was closely followed by a study (Tsuyuki et al., 1968) examining hemoglobin, eye lens, and muscle protein electrophoretic patterns in numerous species of *Sebastes* from both the Atlantic and Pacific, as well as representatives of other scorpaeniform genera. As in Barrett et al. (1966), species-specific patterns were found in hemoglobins, and they interpreted within-species variation as evidence of additional undescribed species. Muscle proteins were not all species-specific, but they separated the 27 species of Pacific *Sebastes* they examined into four subgroups. Comparing these subgroups with the subgenera, little correspondence is seen. Among the 27 species, 11 subgenera are represented. *Sebastes aurora*, the sole member of *Eosebastes*, had a distinct pattern. As in Barrett et al. (1966), there was some coherence among the species of *Pteropodus*; two species (*S. caurinus* and *S. nebulosus*) grouped together as distinct from the other species. However, another species of *Pteropodus* (*S. maliger*) was in a group of 12 species, representing 8 subgenera in which there were no relationships among the species. The muscle and eye lens proteins were distinct at the generic level.

In the early 1970's, Johnson et al. (1970a, b, 1971, 1972) and Johnson (1972) conducted a series of investigations on intraspecific variation in *Sebastes alutus* and other species of *Sebastes*, interspecific variation among *Sebastes*, and intergeneric variation within the Scorpaenidae, using electrophoresis of muscle proteins and several enzymatic systems. Polymorphisms were found in 11 of the 31 species studied. Three patterns were seen in *S. alutus* using two enzyme systems, however these patterns were not related to the geographic distribution of the samples. Among 27 species of *Sebastes* from the Pacific, 10 had unique patterns that allowed them to be identified based on the muscle protein and enzyme systems used in these studies. Several species demonstrated differences in only one enzyme system and thus appeared to be closely related to each other (e.g. *S. reedi* and *S. crameri* and *S. caurinus, S. auriculatus* and *S. maliger*). There was little variation between Atlantic and Pacific *Sebastes*, which were clearly distinct from *Sebastolobus* and *Helicolenus*.

Wishard et al. (1980) used protein electrophoresis to examine within-species relationships among five species of *Sebastes* from the northeast Pacific. Based on allele frequencies at 21 loci, they found evidence of three populations of *S. alutus*, two of *S. pinniger*, and one each of *S. flavidus, S. goodei*, and *S. paucispinis*.

At about the same time, genetic methods were being used in studies on the morphologically similar North Atlantic species of *Sebastes* (Nefyodov, 1971; Naevdal, 1978; Payne and Ni, 1982). A major focus of these studies using electrophoresis of hemoglobin and various enzyme systems was to confirm the presence of more than one sympatric species (*S. mentella, S. fasciatus*, and *S. norvegicus*). More recent work on Atlantic rockfish has employed genetic techniques to identify specimens, particularly juveniles, where more than one species occurs (Nedreaas and Naevdal, 1991; Rubec et al., 1991), and to examine population structure within *S. norvegicus* (Nedreaas et al., 1994).

Electrophoretic studies on Pacific *Sebastes* reached a plateau with the work of Seeb (1986). She analyzed electrophoretic variations of 28 enzymes in 48 species of *Sebastes* and was able to identify all but a few closely related species pairs on the basis of this analysis. She produced phenograms based on genetic distances among the species. As in previous studies (see above), species in some subgenera grouped closely together in these diagrams, while some of the branches contained members of several subgenera. For example, all the members of *Zalopyr, Sebastes*, and *Se-*

bastomus that she considered grouped together, as did most species of *Pteropodus*, and *Sebastodes*. However, species in *Acutomentum*, *Allosebastes*, and *Sebastosomus* were scattered among several lineages within her diagrams. Further work with allozymes of Pacific rockfish investigated population structure within *S. alutus* (Seeb and Gunderson, 1988: little structure was found), and the applicability of allozymes in identifying larval and juvenile specimens (Seeb and Kendall, 1991: allozyme activity and resolution decreased with decreasing size of the fish, but was adequate to aid in identification of juveniles and larvae).

In the 1990's, newer, more powerful genetic techniques were applied to rockfish taxonomic studies in both the Atlantic and northeast Pacific. McGauley and Mulligan (1995) amplified the mitochondrial rRNA (mtDNA) genes of *Sebastes flavidus* using polymerase chain reaction (PCR) and then used restriction fragment length polymorphism (RFLP) analysis to examine population structure. They found essentially no variation in haplotype frequencies among fish collected from Vancouver Island (British Columbia), Westport (Washington), and Cordell Bank (California), indicating that gene flow may be unrestricted within this species throughout its range. They attributed this to long-range dispersal of larvae. However, analysis of a more variable region of the mtDNA may have shown differences that their analysis failed to find. Seeb (1998) investigated gene flow among *S. auriculatus*[3], *S. caurinus*, and *S. maliger* using both allozymes and restriction analysis of mtDNA and found evidence of introgression between all three species in fish from Puget Sound, indicating some level of hybridization.

A major step forward in genetic studies occurred as Rocha-Olivares with others (Rocha-Olivares, 1998a; Rocha-Olivares et al., 1999a, b) began deter-

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[3] *Sebastes auriculatus* is in the subgenus *Auctospina* with *S. dalli*. However, this study and others (e.g. Johnson et al., 1972) indicated it is closely related to other shallow-water deep-bodied spiny rockfishes (e.g. *S. caurinus*) that are in *Pteropodus*.

mining the sequence of nucleotides in the cytochrome *b* gene and part of the control region of the mtDNA molecule (a total of 1,633 bases) in Pacific *Sebastes*, particularly with members of the subgenus *Sebastomus*. These data were then used to address a number of taxonomic and systematic questions. An examination of 14 species of *Sebastomus*, and 40 other species of *Sebastes*, showed that the subgenus was monophyletic. Low levels of divergence in the genetic data indicated recent rapid radiation of the subgenus within the last million years (Fig. 7). Among *Sebastomus*, *S. rosaceus* appeared to represent the oldest lineage, and the rest of the species belonged to one of two clades: a northern clade and a southern clade. Generally, the species pairs produced by the molecular data were the same ones that Chen (1971) found based on morphological data.

Rocha-Olivares (1998b) used multiplex haplotype-specific PCR primers to create subgenus and species-specific assays for portions of the cytochrome-*b* gene in four species in the subgenus *Sebastomus*. He then screened 250 adults representing 31 species of *Sebastes* that had been identified morphologically, and found that with few exceptions, specimens were correctly assigned to species using the primers. Larvae were correctly assigned to the subgenus *Sebastomus*, although none was identified as a species from which the primers were developed. Rocha-Olivares and Vetter (1999) also used sequence data to examine intraspecific variation within *Sebastes helvomaculatus* collected at five sites from Fairweather Bank in the Gulf of Alaska to Cordell Bank off California. They found a high degree of population genetic diversity which could be related to their life history and zoogeography.

The application of genetic techniques is well demonstrated by their resolution of taxonomic problems associated with *Sebastes* from the Southern Hemisphere. *Sebastes* of the Southern Hemisphere has proven to be an exceptional challenge ever since *S. capensis* was placed in the genus by Cuvier and Valenciennes (1829). By the time of Chen's review of *Sebastomus* (Chen, 1971), 11 nominal

species of *Sebastes* had been described from the Southern Hemisphere, all apparently in *Sebastomus*. After reviewing the literature (e.g. De Buen, 1960), and specimens from the west coast of South America and from South Africa, Chen (1971) concluded that more work was needed, but that he would consider all nominal species to be forms of *S. capensis*, as have others (Norman, 1937; Kong Urbina, 1985).

However, Eschmeyer and Hureau (1971) considered the *Sebastes* off the west coast of South America (*S. oculatus*) different from those around south central Atlantic islands and off South Africa (*S. capensis*), and suggested that more than one species occurs off the Pacific coast of South America. Chen (1971) and Eschmeyer and Hureau (1971) both pointed to the limited differentiation of *Sebastes* below the equator as evidence of the difficulty for this Northern Hemisphere, temperate and subarctic genus to cross the tropics.

Based on genetic sequence data, Rocha-Olivares et al. (1999b) found that within the southern clade of *Sebastomus*, *S. constellatus* represented the stock that gave rise to the Southern Hemisphere species: *S. oculatus* off South America and *S. capensis* off Africa. Further genetic studies (Rocha-Olivares et al., 1999c) on Southern Hemisphere *Sebastes* demonstrated that the tropical barrier was crossed successfully only once, and that three lineages (cryptic species?) now exist. The ancestral species is represented by *S. capensis* which occurs off Tristan da Cuhna and South Africa; this lineage is also present in the southwest Atlantic. There are two lineages of *S. oculatus* off the coasts of South America: one off the Pacific coast and the other off the Atlantic coast.

Recent work on the Atlantic species of *Sebastes* has used advanced genetic techniques to investigate relationships among the three morphologically similar sympatric species (e.g. Bentzen et al., 1998; Roques et al., 1999). Bentzen et al. (1998) found an unusual number of tandemly repeated copies of a section of the mtDNA molecule in all three species. The number of tandem repeats (9–17, mean 12.43) was similar in all
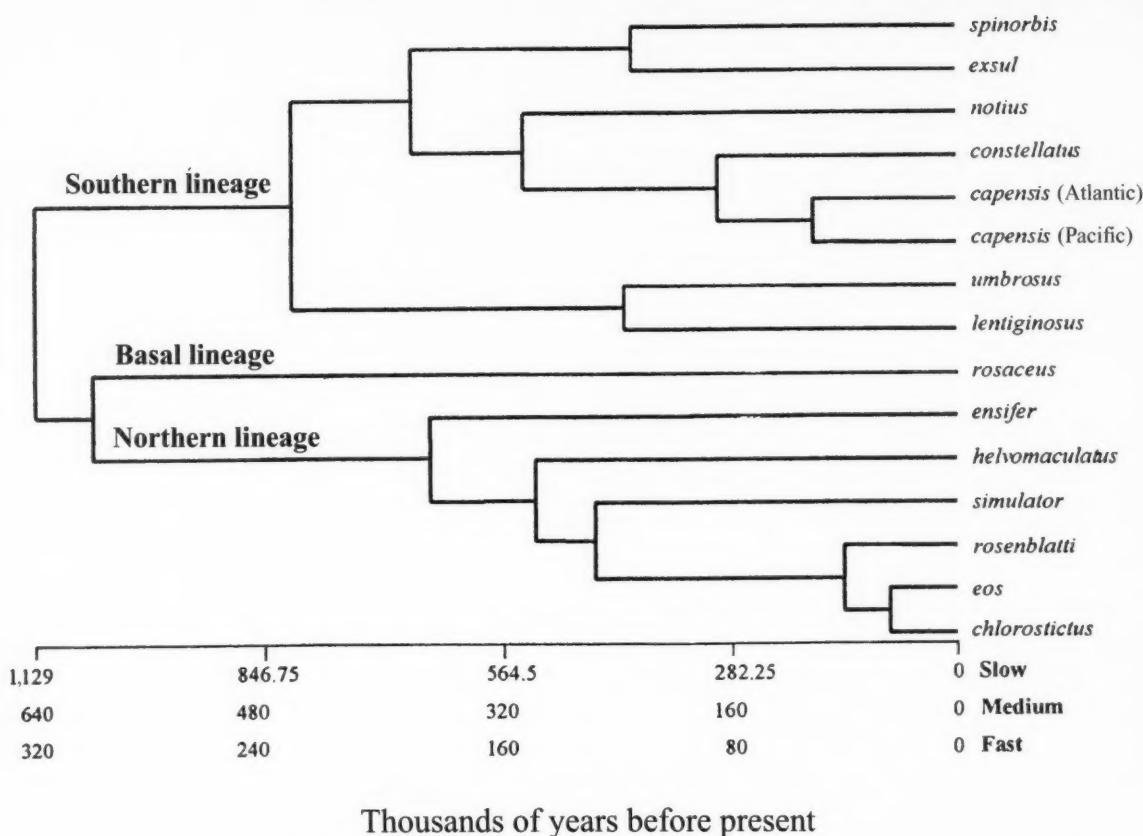
Figure 7.—Relationships among the species in the subgenus *Sebastomus* based on genetic data (from Rocha-Olivares et al., 1999b). Time scales represent different assumed rates of evolution.

three species, suggesting that the duplication might have preceded the divergence of the species. They speculated that the Pacific sister species of the Atlantic species might have homologous repeats. They investigated this hypothesis with *S. aleutianus*, which is another member of the subgenus *Sebastes* according to Barsukov (1981), but did not find the tandem repeats. They suggested that other Pacific species could be examined to determine if they had the tandem repeats and thus might represent the lineage from which the Atlantic species arose. Roques et al. (1999) found that microsatellite data from eight loci could be used to assign individual fish to the correct species more precisely than with other genetic techniques. It was less likely to assign

individuals to the correct population within species. They also concluded, on the basis of shared alleles, that *S. norvegicus* represents the lineage from which the other Atlantic species arose, and that *S. fasciatus* and *S. viviparus* are more closely related to each other than to the other Atlantic species.

As new genetic techniques are developed, they continue to be applied to systematic and taxonomic studies of rockfishes at a variety of levels. For example, Johns and Avise (1998) sequenced the mitochondrial cytochrome-*b* gene from 28 species of rockfish and used these data, as well as the allozyme data of Seeb (1986), to construct molecular phylogenies. They then compared these phylogenies with those of other groups of fishes (Lake Victoria

cichlids and icefishes) in which "species flocks" occur. They found that many of the speciation events in *Sebastes* occurred in clusters in time, and that these events were far more ancient than similar events in African cichlids. They concluded that rockfishes are an ancient species flock, with significant radiation occurring about 5 million years ago (3.6–18 million years ago depending on assumptions concerning rates of evolution).

With the rapid advances in genetic techniques that are now occurring, it is difficult to predict the limits of what will be known of rockfish taxonomy and systematics just a few years from now. However, as more genomic data are accumulated from these phylogenetically interesting fishes, further ad-

Table 1.—*Sebastiscus*, and *Hozukius*, and *Sebastes* subgenera: type species, ranges, numbers of species, and authors.

Subgenus	Type species	Range	No. of species	Authors	Reference
Acutomentum	*ovalis*	NE-NW Pac.	11	Eigenmann and Beeson, 1893	Am. Nat. 27:869
Allosebastes	*sinensis*	NE Pac.-Gulf Calif.	14	Hubbs, 1951	Proc. Biol. Soc. Wash. 64:129-130
Auctospina	*auriculatus*	NE Pac.	2	Eigenmann and Beeson, 1893	Am. Nat. 27:670
Emmelas	*glaucus*	NW Pac.	1	Jordan and Evermann, 1898	Bull. U.S. Natl. Mus. 47:1773
Eosebastes	*aurora*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:430
Hatumeus	*owstoni*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo
Hispaniscus	*rubrivinctus*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:431
Hozukius	*emblemarius*[1]	NW Pac.	2	Matsubara, 1934	J. Imp. Fish. Inst. Tokyo 30:199-210.
Mebarus	*inermis*	NE-NW Pac.	7	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:194
Murasoius	*pachycephalus*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:235
Neohispaniscus	*schlegeli*	NW Pac.	2	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:226
Primospina	*mystinus*	NE Pac.	1	Eigenmann and Beeson, 1893	Am. Nat. 27:669
Pteropodus	*maliger*	NE-NW Pac.	10	Eigenmann and Beeson, 1893	Am. Nat. 27:670
Rosicola	*pinniger*	NE Pac.	3	Jordan and Evermann, 1896	Rep. U.S. Comm. Fish Fish. 1895, pt. 21:429
Sebastes	*norvegicus*	N Atl.	4	Ascanius, 1772	Claude Philibert, pt. 2
Sebastichthys	*nigrocinctus*	NE Pac.	1	Gill, 1862	Proc. Acad. Nat. Sci. Phila. 14:278, 329
Sebastiscus	*marmoratus*	NW Pac.	2	Jordan and Starks, 1904	Proc. U.S. Nat. Mus. 27:91-175
Sebastocarus	*serriceps*	NE Pac.	1	Jordan and Evermann, 1927	Proc. Calif. Acad. Sci., Ser. 4, 16:507
Sebastocles	*hubbsi*	NW Pac.	1	Jordan and Hubbs, 1925	Mem. Carnegie Mus. 10:260.
Sebastodes	*paucispinis*	NE-NW Pac.	5	Gill, 1861	Proc. Acad. Nat. Sci. Phila. 13:165
Sebastomus	*rosaceus*	NE Pac.-S Hemis.	16	Gill, 1864	Proc. Acad. Nat. Sci. Phila. 16:147
Sebastopyr	*rubberimus*	NE Pac.	1	Jordan and Evermann, 1927	Proc. Calif. Acad. Sci., Ser. 4, 16:506
Sebastosomus	*melanops*	NE Pac.	5	Gill, 1864	Proc. Acad. Nat. Sci. Phila. 16:147
Takenokius	*oblongus*	NW Pac.	1	Matsubara, 1943	Trans. Sigenkagaku Kenkyusyo:233
Zalopyr	*aleutianus*	NE-NW Pac.	3	Jordan and Evermann, 1898	Bull. U.S. Natl. Mus. 47:1795

[1] The species name *emblemarius* has been misspelled *embremarius* in several publications including Matsubara (1934, 1943).

vances in our understanding of relationships among them and their evolution are assured.

Present Views on the Subgenera

Although the subgeneric names are mentioned occasionally in recent literature, all but *Sebastomus* still lack rigorous definitions. There is also a lack of agreement concerning the appropriate subgenus for some species (Appendix II). Some species have been assigned to several different subgenera by various authors through the years. For example, *Allosebastes* was erected for *Sebastes sinensis* alone by Hubbs (1951); however, Chen (1986) placed 11 other species in the subgenus, without giving a reason for his action.

Based on the literature, subgeneric names have been assigned to 96 of the currently recognized species of *Sebastes* (Table 1). There are 23 subgenera containing from 1 to 16 species. Nine subgenera contain only one species. Five subgenera have species in both the northwest and northeast Pacific Ocean, six have species only in the northwest Pacific, and ten are exclusively in the northeast Pacific. The North Atlantic contains a subgenus, *Sebastes*, that occurs only there, while the

species in the Southern Hemisphere are in *Sebastomus*, which also occurs in the northeast Pacific. Some of the subgenera have been proposed as genera, and some groups of subgenera have been considered as genera. No rigorous analysis of the validity of the subgenera has yet been attempted, except for *Sebastomus* (Rocha-Olivares, 1999a).

Several field guides and keys for northeast Pacific *Sebastes* have been published (Phillips, 1957; Hitz, 1965; Miller and Lea, 1972; Kramer and O'Connell, 1988; Orr et al., 2000) which assist greatly in identifying the sometimes bewildering array of rockfishes caught even at a single location (Table 2). These guides generally rely on head spine, meristic, morphometric, and color characters that are probably not indicative of systematic relationships among species. The subgenera are usually not mentioned in field guides, although *Sebastomus* is occasionally noted since the species are quite distinctive externally.

Ishida (1984) reviewed what he considered to be the Japanese Sebastinae (*Sebastes*, 26 species; *Helicolenus*, 3 species; *Hozukius*, 2 species; and *Sebastiscus*, 2 species). He included a careful evaluation of all species in these genera that occur around Japan. He summa-

rized his views on the relationships within *Sebastes*, saying ". . . *Sebastes* and *Sebastiscus* of Matsubara (1943) are adopted provisionally and subgenera are not used until world-wide review of these fishes is carried out."

Challenges

Where Does *Sebastes* Belong?

Sebastes is very provisionally placed in the order Scorpaeniformes, suborder Scorpaenoidei, family Sebastidae, subfamily Sebastinae (Nelson, 1994). Much work is yet to be done on the systematics of *Sebastes*, beginning at the ordinal level (is the Scorpaeniformes monophyletic? How does it relate to the Perciformes?). The placement of *Sebastes* within the Scorpaeniformes is presently uncertain. For example, if the Perciformes and Scorpaeniformes had a common ancestor, could it have been similar to *Sebastes*? *Sebastes* and basal perciforms share many characteristics. The hallmark of the scorpaeniforms, the suborbital stay is much reduced in *Sebastes*, and, except for the suborbital stay, *Sebastes* is more similar to basal perciforms than are other scorpaeniforms. In other ways, *Sebastes* is the least specialized of the scorpaeniforms: e.g. head spination is minimal,

Table 2.—Major field guides to identify species of Northeast Pacific *Sebastes*.

Reference	Geographic area	No. of species	Presentation
Clemens and Wilby (1946)	British Columbia.	20	Extended individual species accounts including airbrush monochrome drawings.
Phillips (1957)	California, but ranges of some species extend to Baja California and Alaska.	49	Key to the species and individual species accounts with monochrome photographs.
Clemens and Wilby (1961)	British Columbia.	23	Revision of Clemens and Wilby (1946).
Hitz (1965)[1]	Baja California to the Bering Sea.	53	Species pages arranged by body color and relative length of 2nd and 3rd anal spines. Brief species accounts with black-and-white line sketches and head spine diagrams.
Miller and Lea (1972)	California, but ranges of some species extend to Baja California and Alaska.	58	Brief individual species accounts and a key illustrated with monochrome sketches showing important characters.
Hart (1973)	British Columbia.	33	Key to the species and extended individual species accounts with monochrome drawings.
Eschmeyer et al. (1983)	Coastal waters from the Gulf of Alaska to Baja California.	58	Individual species accounts and color plates annotated with important characters.
Kramer and O'Connell (1988)	Species that occur off Alaska, includes most species from British Columbia, Washington, and Oregon also.	35	Brief individual species accounts including head spine diagrams, sketches of important characters, and color photographs.
Orr et al. (2000)	Northeast Pacific Ocean north of Mexico, including the eastern Bering Sea.	66	Format follows Hitz (1965). Includes individual species accounts and color photographs of most species.

[1] Hitz (1965) was updated, expanded and reprinted three times in informal editions: in 1977, 1981, and 1991.

Table 3.—Characters used to evaluate genera of Sebastidae, following Ishida, 1994.

Characters		States and coding			
Number	Description	Primitive (0)	Intermediate (1)	Derived (2)	Distribution of derived states outside Sebastidae
3	A1 fibers	long		short	Congiopodidae
17	insertion of transversus dorsalis anterior	branched		unbranched	Congiopodidae and occasional elsewhere
41	swimbladder	present		absent	Widespread, especially Scorpaenidae
56	infraorbitals 4 & 5	both present	one present	both absent	Very widespread
64	pharyngobranchials 2 & 3, upper pharyngeal	all separate	pharyngobranchials fused	all fused	Intermediate rare, derived Aploactinidae and Pataecidae
70	number of vertebrae	24		more than 24	Widespread except Setarchidae and Scorpaenidae
80	number of hypurals	2+3	1+3	1+2	Derived states widespread
83	scapula and upper radial	autogenous		fused	Widespread
88	supraneural	1 present		absent	Very widespread

squamation is normal. Is this due to convergence or a common ancestor? Basic unresolved questions regarding the origin and relationships of *Sebastes* and its close relatives include: was their ancestor tropical or boreal, and was it demersal or pelagic? Does *Sebastes* represent the point of divergence that led the demersal-boreal scorpaeniforms away from the pelagic-tropical perciforms, or does the genus represent an end point in scorpaeniform evolution (Washington et al., 1984a)? Although these questions may eventually be resolved using cladistic methodology, the diversity and numbers of species in both the perciforms and scorpaeniforms may continue to deter their resolution.

Within the suborder Scorpaenoidei, Ishida (1994) considered the Sebastidae to contain eight genera. Some members of the Sebastidae have derived states of 9 of the 95 characters that he used to

examine the Scorpaenoidei (Tables 3, 4). All members of the family have derived states of two characters relative to their states in lower percoids, the presumed outgroup of scorpaenoids: the shortening of a1 fibers with the lengthening of the associated maxillary tendon (character 3), and an increase in the number of vertebrae from 24 (character 70) (Table 3).

Within the Sebastidae, the genera *Sebastes, Sebastiscus,* and *Hozukius* share identical character states, resulting in an unresolved trichotomy, which can be given the subfamilial name Sebastinae. This subfamily has the derived states of four characters and shares the derived states of two of these characters with all of the other genera in Sebastidae. However, they do not possess uniquely derived states of any characters. They are united in possessing swimbladders, which is a character

Table 4.—Characters and character states for analysis of Sebastidae, following Ishida, 1994.

Genus	Characters[1]								
	3	17	41	56	64	70	80	83	88
Sebastes	1	0	0	0	0	1	2	1	0
Sebastiscus	1	0	0	0	0	1	2	1	0
Hozukius	1	0	0	0	0	1	2	1	0
Helicolenus	1	0	1	0	0	1	2	1	0
Adelosebastes	1	0	1	0	0	1	2	1	0
Sebastolobus	1	0	1	0	0	1	2	0	0
Trachyscorpia	1	0	1	1	0	1	0	0	0
Plectrogenium	1	1	1	1	1	1	0	0	1

[1] 0=primitive, 1=intermediate, 2=derived.

reversal (in that the rest of the family lacks them, which is the presumed derived state). If *Hozukius* is found to be viviparous like *Sebastes* and *Sebastiscus*, then viviparity would be another derived character to support this subfamily. If *Hozukius* is found to be oviparous, it may be considered the primitive sister genus of *Sebastes* and *Sebastiscus* within the subfamily.

Table 5.—Ecological correlates of characters of *Sebastes*.

Character	Demersal state	Pelagic state
Head spines strength	Strong	Weak
Head spine numbers	Many	Few
Jaw length	Lower > upper	Equal
Interorbital shape	Concave	Convex
Lower pectoral rays	Thick	Not thick
Gill raker length	Short	Long
Jaws scaled	Yes	No
Base of skull	Curved	Flat
Mesethmoid process	Strong	Weak
Color	Red	Black

	Low latitude state	High latitude state
Vertebrae	<29	>28
Dorsal spines	<14	14–15
Dorsal rays	<14	15–16
Anal rays	5	9
Principal caudal rays	13	15
Pectoral rays	17–18	>18

What Morphological Characters Can Be Used for Cladistic Analysis of *Sebastes*?

To be used in a cladistic analysis, morphological characters must be independent of each other and nonadaptive. However, many of the characters used to identify *Sebastes* and used in early attempts to establish relationships among the species are correlated with each other and are adaptive for either pelagic or demersal existence (Table 5).

There is a basic dichotomy in *Sebastes* ecology: species either live in the water column or on the bottom. This is not an absolute; there is a cline between these two basic conditions. Bottom-dwelling species have the lower jaw protruding, eyes close together with a concave interorbital area, heavy armature, thickened pectoral rays, short gill rakers, scaled jaws, and a curved skull base, while pelagic species have opposite states for all of these characters. Convergence toward these character states is expected in species occupying these niches regardless of their ancestry.

Another factor to consider when interpreting characters is that meristic characters tend to show a latitudinal cline: the closer the species lives to the pole, the higher the value (Jordan's Rule: see Lindsey, 1988). This basic pattern is seen in medial fin ray and vertebral counts among species of rockfishes (Table 5). For example, *Sebastiscus*, which lives farther south than most other taxa, has low counts for all

these characters and *Emmelas*, which lives in the northern part of the range, has higher counts. The species of *Sebastomus*, which live primarily in the southern part of the range of *Sebastes* in the northeast Pacific, including the Gulf of California, and the Southern Hemisphere, have lower medial fin ray counts than most other *Sebastes*. The Atlantic species of *Sebastes* have the highest vertebral counts in the genus, and presumably they originated from species that traversed the Arctic Ocean from the Pacific.

Can Early Life History Information Be Applied to the Problem?

Scorpaenoids display a variety of reproductive patterns, but the use of information on reproduction in systematic studies is limited, since the patterns are unknown in several genera (Washington et al., 1984b). While most scorpaenoids share ovoviviparity with most other teleosts, *Sebastes*, *Sebastiscus*, and possibly *Helicolenus* share the unique pattern of internal fertilization, intraovarian embryological development with maternal contribution to nutrition, and production of many (~10^5) newly hatched, undeveloped larvae. The reproductive pattern of *Hozukius* is unknown, although the anal anatomy is that of a live-bearer (Ida[4]). As opposed to the widespread pattern of producing individual planktonic eggs, several scorpaenid genera (*Sebastolobus*, *Pterois*, *Scorpaena*) extrude eggs in a floating bilobed gelatinous egg mass. A single oil globule is present in eggs of *Pterois* and *Sebastolobus*, while none is present in the eggs of *Scorpaena* or *Dendrochirus*.

The larvae of many scorpaeniforms, including the scorpaenoids, have parietal and other head spines, which are not seen in larvae of other fishes. In *Sebastolobus* and *Scorpaenodes* the parietal ridge is enlarged and ends in a bifid spine, with the posterior part (the nuchal spine) being predominant, whereas in *Sebastes*, *Sebastiscus* (Okiyama, 1988), and *Helicolenus* the parietal spine is

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[4] Ida, Hitoshi, Kitasato Univ., Sanriku, Jpn., personal commun., 20 January 1999.

larger and slightly separate from the nuchal spine (Moser et al., 1977; Moser, 1996). There is a tendency for early development of pectoral fins in scorpaeniforms, and in some groups the pectoral fins are quite pronounced in the larvae. Pronounced pectoral fins are seen in *Sebastolobus*, *Scorpaenodes*, *Ectreposebastes* and some species of *Sebastes* (e.g. *S. levis*). Larvae of *Helicolenus* develop a spongy mass of tissue anteriorly along the dorsal midline. Once the larvae of more scorpaenoids become known, such characters will prove invaluable in systematic studies of the group.

Within the genus *Sebastes*, the preflexion-extrusion larvae of most species are known (Matarese et al., 1989; Moser, 1996). These can be obtained fairly easily, and their identity known, by collecting pregnant females and extruding the larvae. Aside from some shared characteristics among preflexion larvae of species of *Sebastomus*, the appearance of these larvae seems to offer little taxonomic or systematic promise. There is considerable overlap in characters among species in these larvae and considerable within-species variation.

Later-stage larvae of *Sebastes* are distinctive from larvae of other fishes, but many share characters with each other that prevent identifying them to species in all but a few cases. Larval characters that may be useful in taxonomy and systematics include body shape, pigment patterns, and the development and subsequent reduction or loss of head spines (Kendall, 1991). As with early larvae, the later larvae of *Sebastomus* share some characters that distinguish them from other *Sebastes* larvae, but within the subgenus, the larvae of many species are quite similar. It appears that larvae of *Pteropodus* may also share some characters, but the larvae of several species are still unknown. A few other species have distinctive larvae (e.g. *Sebastes paucispinis*, *S. jordani*, *S. melanostomus*, and *S. levis*), but their morphology does not seem to be related to their subgeneric placement. There are some intriguing similarities among the larvae of some species of *Sebastes* that may indicate

relationships not otherwise suggested (e.g. the larvae of *S. jordani*, *S. alutus*, and *S. polyspinis* from the Pacific all look quite similar to the larvae of the Atlantic species of *Sebastes*).

As juveniles, *Sebastes* are morphologically quite different from the larvae and the adults. Some species reside in the water column, some associate with flotsam or school, and some take up a demersal existence (Moser and Boehlert, 1991). The observed pigment patterns of juveniles may be adaptive for these various modes of existence, so caution is advised when using them in systematic analysis.

Clearly the early life history of scorpaenoids in general and *Sebastes* in particular offers a large number of characters to apply to systematic studies. However, until the reproductive patterns and early life history series of more species are described, this potential cannot be realized.

Conclusions

After a period of discovering the incredible diversity of *Sebastes* in the middle 1800's, the history of the systematics of the genus was marked by bitter debate in the late 1800's over relationships among the species. With few exceptions (e.g. *S. carnatus-S. chrysomelas-S. atrovirens*, and *S. ciliatus*) the species of *Sebastes* are now well-defined, and few new ones are being described (Kim and Lee, 1994; Eitner et al., 1999). However, little recent work has been done on the genus as a unit, and its systematics remain in a confused state, with over 100 species, and very little obvious structure within the genus. What other fish genus contains so many species, but with such little indication of structure within it? Beyond the fairly cohesive group *Sebastomus* and a few species pairs (e.g. *Sebastes fasciatus/S. mentella*, *S. babcocki/S. rubrivinctus*, *S. serranoides/S. flavidus*), practically any two species look as similar to each other as to any other species.

In order to progress in our understanding of the relationships within this interesting, and ecologically and economically important group of fishes, traditional gross morphological as well as novel characters, such as those avail-

able through genetics, need to be evaluated more rigorously. With the incredible size of the genus and its wide distributional range, this will be an enormous task.

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Appendix I

Original Definitions of *Sebastes*, *Hozukius*, and *Sebastiscus*, and the Subgenera of *Sebastes*

Sebastes Cuvier (1829), type species: *S. norvegicus*: "Have all the characters of the *Scorpaena* except that they lack cutaneous filaments, and that their head, less covered with bristles, is scaly.

"There is a large species of them in the North Sea, called 'marulke,' and in some places 'carp' (*Sebastes norvegicus*, Nob., *Perca marina*, Pennt., *Perca norvegica*, Müll.), Bonnat. Encycl. Meth., plate on ichthyology, fig. 210. It is red, and is often more than two feet long. It is dried to make food provisions. Its dorsal spines are used as needles by Eskimos.

"The Mediterranean has a species very similar, but its dorsal rays are less numerous (*Sebastes imperialis*, Nob., *Scorpaena dactyloptera*, Laroche, Annales Mus., 13, plate 22, fig. 9). Its palate is black; it lacks a swim bladder, although the preceding species has one."[2]

Sebastodes Gill (1861), type species: *S. paucispinis*: "A very different facies from *Sebastes*, and is readily distinguished by the longer body, the very protuberant lower jaw, which has a symphyseal swelling beneath, the very minute scales, the form and armature of the head, the deep emargination of the dorsal fin and the emarginated caudal."

Sebastichthys Gill (1862b), type species: *S. nigrocinctus*: "Species referred to the genus *Sebastes*, which has eleven to twelve (XI.+1.–XII.+1.) spines in its first dorsal fin, palatine teeth, and the physiognomy of *Sebastes* (*norvegicus*)."

Sebastomus Gill (1864), type species: *S. rosaceus*: "Distinguished by the texture of the bones of the skull, armed orbital ridges, prefrontals &c."

Sebastosomus Gill (1864), type species: *S. melanops*: ". . . the genus *Sebastichthys* includes at least three genera. The *Sebastichthys nigrocinctus* is somewhat related to *Scorpaena*, and distinguished by elevated, serrated coronal crests. The other California species represented by the *Sebastes melanops*, seen by me, differ so much that they may be sep-arated and combined under the genus *Sebastosomus . . .*"

Acutomentum Eigenmann and Beeson (1893), type species: *S. ovalis*: Taken from their key: "Parietals meeting above the supra-occipital. Lower jaw much projecting; head broad, the skull usually convex; cranial ridges, when present, low; gill rakers very long and slender; scales usually smooth, few if any accessory scales. Parietal ridges ending in spines; preocular, supraocular and tympanic spines well developed. Peritoneum black. Postocular spine present. Second anal spine usually stronger and longer than third. Symphyseal knob strong, projecting forward. Dorsal low. (Peritoneum black, mandibles and maxillary scaled)."

Primospina Eigenmann and Beeson (1893), type species: *S. mystinus*: Taken from their key: "Parietals meeting above the supra-occipital. Lower jaw much projecting; head broad, the skull usually convex; cranial ridges, when present, low; gill rakers very long and slender; scales usually smooth, few if any accessory scales. Postocular spine not developed. Parietal ridges not ending in spines. Preocular spines well developed. Supraocular and tympanic spines sometimes present. Interorbital wide, convex. Peritoneum black. Approximated edges of sub-opercle, and interopercle frequently ending in spines.

Pteropodus Eigenmann and Beeson (1893), type species: *S. maliger*: Taken from their key: Parietals separated by the supra-occipital. Cranium with many ridges, all ending in spines. Postocular spines wanting. Coronal spines none.

Auctospina Eigenmann and Beeson (1893), type species: *S. auriculatus*: Taken from their key: Parietals separated by the supra-occipital. Cranium with many ridges, all ending in spines. Postocular spines wanting. Coronal spines present.

Eosebastes Jordan and Evermann (1896), type species: *S. aurora*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Hispaniscus Jordan and Evermann (1896), type species: *S. rubrivinctus*: No description of the subgenus of-fered; see description of type species in Jordan and Evermann (1898).

Rosicola Jordan and Evermann (1896), type species: *S. pinniger*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Emmelas Jordan and Evermann (1898), type species: *S. glaucus*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Zalopyr Jordan and Evermann (1898), type species: *S. aleutianus*: No description of the subgenus offered; see description of type species in Jordan and Evermann (1898).

Sebastiscus Jordan and Starks (1904), type species: *Sebastiscus marmoratus*: "This genus is based on species having the external appearance of *Sebastodes* and much resemblance to the subgeneric group called *Pteropodus*, but having 12 spines in the dorsal fin and the vertebrae 10+14=24, agreeing in these regards with *Scorpaena*. From *Helicolenus*, *Sebastiscus* differs, solely, perhaps, in the presence of a well-developed air-bladder. Peritoneum pale."

Sebastocles Jordan and Hubbs (1925), type species: *S. elegans* (=*S. hubbsi*): "Dorsal spines low, normally fourteen; interorbital deeply concave, size small."

Sebastocarus Jordan and Evermann (1927), type species: *S. serriceps*: "This genus is closely allied to *Sebastichthys* from which it differs in the more compressed body and especially in the strict and high ridges on the head, all of them being free from serrations or accessory tubercles."

Sebastopyr Jordan and Evermann (1927), type species: *S. ruberrimus*: "This genus is allied to *Sebastomus*, but of much coarser build, the cranial spines in the adult being rough with blunt spinules."

Hozukius Matsubara (1934), type species: *H. emblemarius*: "External: Body rather robust and somewhat compressed. Maxillary, and mandible covered with small ctenoid scales but not on branchiostegals. Teeth in villiform bands on vomer and palatines. Head much

spinous; nasal, preocular, supraocular, postocular, tympanic, coronal, parietal, and nuchal spines present; upper and posterior margins of orbit provided with many accessory spines; parietal ridge not conspicuous. Orbital margins of preorbital and second suborbital bones armed with a sharp spine which is directed backward; first suborbital margined with several small spines; lower border of preorbital with two very strong, sharp bifid spines. Lower three preopercular spines much larger than upper two; subopercle and interopercle each with a small, sharp spine at their approximation. Symphyseal knob very large. Dorsal with 12 spines and about 12 rays; anal with 3 spines and about 6 rays. Auxillary flap absent.

"Internal: Skull thick and heavy. Base of skull (parasphenoid) moderately curved. Frontal, parietal, pterotic and supratemporal much cavernous resembling a bee-hive in general appearance. Parietals entirely meeting; upper margin of orbit and frontal ridges somewhat raised. Mesethmoid processes directed upward and forward. Nodule on the front of prefrontal for the articulation with palatine well developed. Ventral process of basisphenoid rudimentary, not reaching to paraspheniod; basisphenoid with a small pore between it and basis crania. Myodome well developed, with a rather large posterior opening. Second suborbital bone very broad and long entirely touching to the upper ridge of preopercle; third and fourth suborbital bones present. Gill-rakers long and stout, the longest one much longer than the longest gill-lamella. Vertebrae 9 + 16 + hypural = 26; parapophysis developed from the sixth vertebra, its processes widely diverging, directed outward and downward. Air bladder absent. Peritoneum jet black."

Hatumeus Matsubara (1943), type species: *S. owstoni*: "Cranium thin and papery; interorbital space and occiput flat, the former about 3.3 times in base of the cranium; preocular, postocular, tympanic and parietal spines present, but small and weak; nuchal spines sometimes present; supraocular and coronal spines absent; cranial ridges

absent except for the parietal ridges which are low but never scaled over; parietals separated; mesethmoid processes never directed upward; base of cranium markedly curved; ventral process of basisphenoid feeble, never attached to the parasphenoid; nasal spines low, but strong; preorbital lobes without spines; second suborbital bone much wider than long. Vertebrae usually 30 including the hypural. Peritoneum jet black. Gill-rakers long and slender. Dorsal mostly XIV, 14; anal usually III, 9 to 10. Lower jaw strongly produced beyond the upper when the mouth is closed; symphyseal knob evident; jaws thickly covered by small scales."

Mebarus Matsubara (1943), type species: *S. inermis*: "Cranium rather thin; interorbital space and occiput plain or very slightly convex, the former about 3.0 times in base of the cranium; preocular spines always present; supraocular and parietal spines small or absent; postocular, tympanic and nuchal spines entirely absent; cranial ridges absent except for the parietal which is very low and sometimes scaled over; parietals widely separated; mesethmoid processes depressed or slightly directed upward; base of cranium strongly curved; ventral process of basisphenoid feeble; nasal spines low, but strong. Vertebrae usually 26 or 27 including the hypural. Peritoneum black or pale. Gill-rakers long and slender. Dorsal spines 13. Lower jaw projecting far beyond the upper, provided with a prominent symphyseal knob; maxillary at least scaly; preorbital lobes with or without spines.

"The present new subgenus is closely related to the subgenus *Rosicola*, but differs from it in having weak parietal ridges and flattish interorbital space and lacking the postocular and tympanic spines. The subgenus is also separable from *Sebastosomus* in having usually the strong preocular spine, flattish interorbital space and parietals widely separated."

Murasoius Matsubara (1943), type species: *S. pachycephalus*: "Cranium very thick and heavy; interorbital space deeply concave, about $3^{1}/_{2}$ in base of cranium; cranial spines broad and stout,

the pointed tips directed backward; preocular, postocular, tympanic and parietal spines present; supraocular, coronal and nuchal spines absent; supraocular ridges exceedingly high and stout, forming a narrow flat area between them; frontal ridges barely evident, can not be seen without elimination of the skin; parietal ridges broad and high, but a little lower than the supraocular ridges; nasal spines stout, directed upward and slightly backward; mesethmoid processes strongly compressed, directed forward and upward; parietal bones separated; base of cranium straight; ventral process of basisphenoid entirely meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum white. Air-bladder entirely free from the layer of connective tissue lying outside the peritoneum, the bladder being easily detached from the coelom; the extrinsic muscle band of the bladder gives rise posteriorly to a single short ligament; the anterior part of the muscle band not pierced through by a ligament. Gill-rakers very short and blunt. Dorsal spines 13. Jaws, snout and branchiostegals mostly naked; upper jaw projecting beyond the lower when mouth is closed; symphyseal knob at the tip of lower jaw absent or barely evident."

Neohispaniscus Matsubara (1943), type species: *S. schlegelii*: "Skull thick and heavy; interorbital space flat or slightly convex, its width about 2.6 to 3.3 times in base of the cranium; cranial spines well developed, directed straightly backward; preocular, postocular, tympanic and parietal spines always present supraocular, corneal and nuchal spines absent; parietal ridges high and naked; frontal ridges low but distinct, the space between them shallowly concave; supraocular edges low or depressed. as high as or lower than the frontal ridges; mesethmoid processes slightly elevated upward; base of cranium some-what curved; parietals separated or partly meeting; ventral process of the basisphenoid well developed, entirely meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum usually white. Gill-rakers, comparatively long and slender with pointed

tips. Lower jaw generally projecting beyond the upper when the mouth is closed, with a rather small symphyseal knob. Jaws usually naked.

"The present subgenus is closely related to *Hispaniscus*, but differs from it in having a much longer and wider interorbital space, elevated mesethmoid processes and shallowly depressed area between the frontal ridges."

Takenokius Matsubara (1943), type species: *S. oblongus*: "Cranium thick and heavy; interorbital space and occiput flat or slightly convex, the former about 3.7 times in base of cranium; postocular, tympanic and parietal spines present, directed backward and downward; preocular supraocular, coronal and nuchal spines entirely absent; parietal ridges low but broad; supraocular edges depressed, never higher than the frontal ridges; frontal ridges low, the space between them flattish, never deeply concave; mesethmoid processes directed forward and upward; parietals meeting or narrowly separated; the patch of vomerine teeth triangular; base of cranium straight; ventral process of basisphenoid meeting the parasphenoid. Vertebrae 26 including hypural. Peritoneum pale. Gill-rakers very short, tubercular. Jaws equal in length and entirely scaleless; symphyseal knob inconspicuous."

Allosebastes Hubbs (1951), type species: *S. sinensis*: "... reduction of the anal soft-rays to 5.... smooth, mostly cycloid scales; the unswollen lower pectoral rays; the excessively long anal spines (the second extends well beyond the longest soft-ray); the closely clumped subparallel upper 3 preopercular spines (the lower 2 are well separated and divergent); the protuberant posterior end of the mandible, almost resembling a flat spine; and, especially, the very firm well-exposed suborbital stay (second suborbital), with the bone widened about the unusually large pore, which has a somewhat raised and roughened rim."

Summary of Nomenclature
of *Sebastes* Listed Alphabetically
by Subgenus

Original species[1]	Authors	Date	Present species[2]	Common name	Eigenmann and Beeson, 1894
	(Fitch)	1964	*phillipsi*	chameleon rockfish	
	Lea and Fitch	1979	*melanosema*	semaphore rockfish	
	(Westrheim and Tsuyuki)	1967	*reedi*	yellowmouth rockfish	
	Barsukov	1988	*cheni*		
	(Taranetz and Moiseev)	1933	*polyspinis*	northern rockfish	
	Kim and Lee	1994	*koreanus*	hwanghee-bolnak	
	Eitner et al.	1999	*moseri*	whitespeckled rockfish	
alutum	(Gilbert)	1890	*alutus*	Pacific ocean perch	*Acutomentum*
brevispine	(Bean)	1884	*brevispinis*	silvergray rockfish	*Pteropodus*
clavilatum	Starks	1911	*(?)*		
eigenmanni	Cramer	1896	*(?)*		
entomelas	(Jordan and Gilbert)	1880	*entomelas*	widow rockfish	*Primospina*
	(Cramer)	1895	*hopkinsi*	squarespot rockfish	
	(Eigenmann and Beeson)	1893	*macdonaldi*	Mexican rockfish	*Acutomentum*
ovale	(Ayres)	1863	*ovalis*	speckled rockfish	*Acutomentum*
rufum	(Eigenmann and Eigenmann)	1890	*rufus*	bank rockfish	*Sebastomus*
	(Jordan and Starks)	1904	*flammeus*	sankou-menuke	
	(Jordan and Starks)	1904	*iracundus*	oo-saga	
	(Jordan and Snyder)	1900	*scythropus*	ukeguchi-mebaru	
	(Wakiya)	1917	*baramenuke*	bara-menuke	
paucispinosus	Matsubara	1943	*(alutus)*		
	Chen	1975	*varispinis*		
	Chen	1975	*peduncularis*		
	(Beebe and Tee-Van)	1938	*cortezi*		
	(Gilbert)	1890	*sinensis*		*Pteropodus*
	Quast	1971	*variegatus*	harlequin rockfish	
	Lea and Fitch	1972	*rufinanus*	dwarf-red rockfish	
	(Gilbert)	1890	*diploproa*	splitnose rockfish	*Sebastichthys*
	(Starks)	1911	*emphaeus*	Puget Sound rockfish	
prorigerum	(Jordan and Gilbert)	1880	*proriger*	redstripe rockfish	*Pteropodus*
	(Gilbert)	1890	*saxicola*	stripetail rockfish	*Pteropodus*
	(Gilbert)	1897	*semicinctus*	halfbanded rockfish	
	(Gilbert)	1915	*wilsoni*	pygmy rockfish	
	(Gilbert)	1890	*zacentrus*	sharpchin rockfish	*Pteropodus*
dallii	(Eigenmann and Beeson)	1894	*dalli*	calico rockfish	*Pteropodus*
auriculata	Girard	1854	*auriculatus*	brown rockfish	*Auctospina*
	Hilgendorf	1880	*glaucus*	kuro-menuke	
	(Gilbert)	1890	*aurora*	aurora rockfish	*Auctospina*
	(Jordan)	1897	*crameri*	darkblotched rockfish	
deani	Starks	1911	*(?)*		
introniger	(Gilbert)	1890	*(melanostomus)*		*Acutomentum*
	(Eigenmann and Eigenmann)	1890	*melanostomus*	blackgill rockfish	*Acutomentum*
rupestris	(Gilbert)	1890	*(melanostomus)*		*Sebastomus*
	(Jordan and Thompson)	1914	*owstoni*	hatsume	
	Ayres	1859	*elongatus*	greenstriped rockfish	
	(Eigenmann and Eigenmann)	1889	*levis*	cowcod	*Sebastomus*
	(Jordan and Gilbert)	1880	*rubivinctus*	flag rockfish	*Sebastichthys*
atrorubens	(Gilbert)	1898	*(atrovirens)*		
	(Jordan and Gilbert)	1880	*atrovirens*	kelp rockfish	*Pteropodus*
	(Jordan and Hubbs)	1925	*thompsoni*	usu-mebaru	
	(Matsubara)	1934	*wakiyai*	gaya-modoki	
	Cuvier and Valenciennes	1829	*inermis*	mebaru	
	Gunther	1878	*joyneri*	togotto-mebaru	
taczanowskii	(Steindachner)	1880	*taczanowski*	ezo-mebaru	
	Barsukov	1972	*minor*	aka-gaya	
guentheri	(Jordan and Starks)	1904	*(inermis)*		
paradoxus	Matsubara	1943	*(wakiyai)*		
tokionis	(Jordan and Starks)	1904	*(inermis)*		
	Matsubara	1943	**nudus*		
	Temminck and Schlegel	1843	*pachycephalus*	mura-soi	
	(Schmidt)	1931	**nigricans*		
	Matsubara	1943	**chalcogrammus*		
	Hilgendorf	1880	*schlegeli*	kuro-soi	
	Steindachner and Doderlein	1884	*vulpes*	kitsune-mebaru	

Major generic or subgeneric assignments			Other subgeneric assignments		Current subgenus
Jordan and Evermann, 1898	Jordan, Evermann, and Clark, 1930	Matsubara, 1943	Reference	Subgenus	
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
				Unknown	Unknown
Acutomentum	Acutomentum	Acutomentum			Acutomentum
Acutomentum	Acutomentum				Acutomentum
	Acutomentum				Acutomentum
Acutomentum	Acutomentum				Acutomentum
Acutomentum	Acutomentum		Chen, 1986	Acutomentum	Acutomentum
Acutomentum	Acutomentum		Chen, 1986	Acutomentum	Acutomentum
Acutomentum	Acutomentum				Acutomentum
Acutomentum	Acutomentum		Chen, 1986	Acutomentum	Acutomentum
Acutomentum	Acutomentum		Chen, 1986	Acutomentum	Acutomentum
		Acutomentum			Acutomentum
		Acutomentum			Acutomentum
		Acutomentum			Acutomentum
		Acutomentum			Acutomentum
		Acutomentum			Acutomentum
			Chen, 1986	Allosebastes	Allosebastes
			Chen, 1986	Allosebastes	Allosebastes
			Chen, 1986	Allosebastes	Allosebastes
Hispaniscus	Hispaniscus		Hubbs, 1951; Chen, 1986	Allosebastes	Allosebastes
			Chen, 1986	Allosebastes	Allosebastes
					Allosebastes
Eosebastes	Eosebastes		Chen, 1986	Allosebastes	Allosebastes
	Eosebastes		Chen, 1986	Allosebastes	Allosebastes
Acutomentum	Acutomentum		Chen, 1986	Allosebastes	Allosebastes
Eosebastes	Eosebastes		Chen, 1986	Allosebastes	Allosebastes
Eosebastes	Acutomentum		Chen, 1986	Allosebastes	Allosebastes
Hispaniscus	Hispaniscus		Chen, 1986	Allosebastes	Allosebastes
	Auctospina				Auctospina
Auctospina	Auctospina				Auctospina
Emmelas	Emmelas	Emmelas			Emmelas
Eosebastes	Eosebastes				Eosebastes
Eosebastes	Eosebastes				Eosebastes
	Eosebastes				Eosebastes
Eosebastes	Eosebastes				Eosebastes
Eosebastes	Eosebastes				Eosebastes
Sebastomus	Sebastomus				Eosebastes
		Hatumeus			Hatumeus
Hispaniscus	Hispaniscus				Hispaniscus
Hispaniscus	Hispaniscus				Hispaniscus
Hispaniscus	Hispaniscus				Hispaniscus
Zalopyr	Zalopyr				Mebarus
Zalopyr	Zalopyr				Mebarus
		Mebarus	Chen, 1985; 1986	Mebarus	Mebarus
		Mebarus	Chen, 1985; 1986	Mebarus	Mebarus
		Mebarus	Chen, 1985	not Mebarus	Mebarus
		Mebarus	Chen, 1985; 1986	Mebarus	Mebarus
		Mebarus	Chen, 1985	not Mebarus	Mebarus
					Mebarus
		Mebarus			Mebarus
		Mebarus			Mebarus
		Mebarus			Mebarus
		Murasoius			Murasoius
		Murasoius			Murasoius
		Murasoius			Murasoius
		Murasoius			Murasoius
		Neohispaniscus			Neohispaniscus
		Neohispaniscus	Chen, 1986	Takenokius	Neohispaniscus

Appendix II (continued)

Original species[1]	Authors	Date	Present species[2]	Common name	Eigenmann and Beeson, 1894
ijimae	(Jordan and Metz)	1913	*(vulpes)*		
zonatus	Chen and Barsukov	1976	*(vulpes)*		
	(Jordan and Gilbert)	1880	*carnatus*	gopher rockfish	*Pteropodus*
	Richardson	1844	*caurinus*	copper rockfish	*Pteropodus*
	(Jordan and Gilbert)	1881	*chrysomelas*	black-and-yellow rockfish	*Pteropodus*
gilberti	Cramer	1896	*(dalli)*		
	(Jordan and Gilbert)	1880	*maliger*	quillback rockfish	*Pteropodus*
	Ayres	1854	*nebulosus*	China rockfish	*Pteropodus*
	(Jordan and Gilbert)	1880	*rastrelliger*	grass rockfish	*Pteropodus*
vexillaris	(Jordan and Gilbert)	1880	*(caurinus)*		*Pteropodus*
	Hilgendorf	1880	*nivosus*	goma-soi	
	Hilgendorf	1880	*trivittatus*	shima-zoi	
	(Matsubara)	1937	*hubbsi*	yoroi-mebaru	
	(Matsubara)	1934	*longispinis*	kourai-yoroi mebaru	
alexandri	(Evermann and Goldsborough)	1907	*(auriculatus)*		
	(Thompson)	1915	*babcocki*	redbanded rockfish	
	(Jordan and Gilbert)	1880	*miniatus*	vermilion rockfish	*Sebastomus*
	(Gill)	1864	*pinniger*	canary rockfish	*Sebastomus*
	(Travin)	1951	*mentella*	deepwater redfish	
	Storer	1854	*fasciatus*	Acadian redfish	
norvegica	(Ascanius)	1772	*norvegicus*	golden redfish	
	Kroyer	1845	*viviparus*	Norway haddock	
	Ayres	1859	*nigrocinctus*	tiger rockfish	*Sebastichthys*
albo-fasciatus	(Lacepede)	1802	*albofasciatus*	ayame-kasago	
	(Cuvier and Valenciennes)	1829	*marmoratus*	kasago	
tertius	(Barsukov and Chen)	1978	*(marmoratus)*		
	(Jordan and Gilbert)	1880	*serriceps*	treefish	*Sebastichthys*
	(Eigenmann and Eigenmann)	1890	*goodei*	chilipepper	*Sebastodes*
	(Gilbert)	1896	*jordani*	shortbelly rockfish	
	Ayres	1854	*paucispinis*	bocaccio	*Sebastodes*
	(Jordan and Starks)	1904	*itinus*	yanagi-mebaru	
	Hilgendorf	1880	*steindachneri*	yanagi-no-mai	
	Chen	1975	*spinorbis*		
	Chen	1971	*exsul*		
	Chen	1971	*simulator*	pinkrose rockfish	
	Chen	1971	*rosenblatti*	greenblotched rockfish	
	Chen	1971	*ensifer*	swordspine rockfish	
	Chen	1971	*notius*		
	Ayres	1859	*helvomaculatus*	rosethorn rockfish	*Sebastomus*
	Chen	1971	*lentiginosus*	freckled rockfish	
ayresii	(Gilbert and Cramer)	1897	*(rosaceus)*		
	(Jordan and Gilbert)	1880	*chlorostictus*	greenspotted rockfish	*Sebastomus*
	(Jordan and Gilbert)	1880	*constellatus*	starry rockfish	*Sebastomus*
	(Eigenmann and Eigenmann)	1890	*eos*	pink rockfish	*Sebastomus*
gillii	(Eigenmann)	1891	*gilli*	bronzespotted rockfish	*Sebastomus*
rhodochloris	(Jordan and Gilbert)	1880	*(helvomaculatus)*		*Sebastomus*
	Girard	1854	*rosaceus*	rosy rockfish	*Sebastomus*
	(Jordan and Gilbert)	1882	*umbrosus*	honeycomb rockfish	*Sebastomus*
	Valenciennes	1833	*oculatus*		
	(Gmelin)	1789	*capensis*		
chamaco	(Evermann and Radcliffe)	1917	*(capensis)*		
	(Tilesius)	1813	*ciliatus*	dusky rockfish	*Sebastosomus*
	(Ayres)	1862	*flavidus*	yellowtail rockfish	*Sebastosomus*
	Girard	1856	*melanops*	black rockfish	*Sebastosomus*
	(Jordan and Gilbert)	1881	*mystinus*	blue rockfish	*Primospina*
	(Eigenmann and Eigenmann)	1890	*serranoides*	olive rockfish	*Sebastosomus*
	(Jordan and Gilbert)	1883	*ruberrimus*	yelloweye rockfish	
	Gunther	1877	*oblongus*	takenoko-mebaru	
	Barsukov	1970	*borealis*	shortraker rockfish	
	(Jordan and Evermann)	1898	*aleutianus*	rougheye rockfish	
kawaradai	(Matsubara)	1934	*(aleutianus)*		
melanostictus	(Matsubara)	1934	*(aleutianus)*		
swifti	(Evermann and Goldsborough)	1906	*(aleutianus)*		
	Hilgendorf	1880	*matsubarae*	akou-dai	

[1] Listed when different from present species name.

[2] ( )=synonomyzed with; °=form of *pachycephalus*.

Major generic or subgeneric assignments			Other subgeneric assignments		Current subgenus
Jordan and Evermann, 1898	Jordan, Evermann, and Clark, 1930	Matsubara, 1943	Reference	Subgenus	
		Neohispaniscus	Chen, 1986	Takenokius	Neohispaniscus
			Chen, 1986	Takenokius	Neohispaniscus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
Pteropodus	Pteropodus				Pteropodus
		Pteropodus	Chen, 1986	Takenokius	Pteropodus
		Pteropodus	Chen, 1986	Takenokius	Pteropodus
		Pteropodus	Jordan and Hubbs, 1925	Sebastocles	Pteropodus
		Pteropodus			Pteropodus
	Rosicola				Rosicola
	Rosicola				Rosicola
Rosicola	Rosicola				Rosicola
Rosicola	Rosicola				Rosicola
					Sebastes
					Sebastes
		Sebastes			Sebastes
		Sebastes			Sebastes
Sebastichthys	Sebastichthys				Sebastichthys
			Matsubara, 1943	Sebastiscus	Sebastiscus
			Matsubara, 1943	Sebastiscus	Sebastiscus
			Chen, 1986	Sebastiscus	Sebastiscus
Sebastichthys	Sebastocarus				Sebastocarus
Sebastodes	Sebastodes				Sebastodes
Sebastodes	Sebastodes				Sebastodes
Sebastodes	Sebastodes				Sebastodes
		Sebastodes			Sebastodes
		Sebastodes			Sebastodes
			Chen, 1975	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
					Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
Sebastomus	Sebastomus				Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
			Chen, 1971	Sebastomus	Sebastomus
Primospina	Sebastosomus				Sebastosomus
Sebastosomus	Sebastosomus				Sebastosomus
Sebastosomus	Sebastosomus				Sebastosomus
Primospina	Sebastosomus				Sebastosomus
Sebastosomus	Sebastosomus				Sebastosomus
Sebastomus	Sebastopyr				Sebastropyr
		Takenokius	Chen, 1986	Takenokius	Takenokius
					Zalopyr
Zalopyr	Zalopyr				Zalopyr
		Zalopyr			Zalopyr
		Zalopyr			Zalopyr
	Eosebastes				Zalopyr
		Zalopyr			Zalopyr

Reef Habitats in the Middle Atlantic Bight: Abundance, Distribution, Associated Biological Communities, and Fishery Resource Use

FRANK W. STEIMLE and CHRISTINE ZETLIN

Introduction

Spatial distribution and perhaps the abundance of fishery resources are influenced by physical and other habitat factors. The identification of significant marine habitats and strong or critical associations between living marine resources (LMR's) and these habitats can lead to a better understanding of how environmental influences affect LMR's and fisheries and support their management (NMFS, 1999a).

The Middle Atlantic Bight (the area of the U.S. east coast and continental shelf between Cape Cod, Mass., and Cape Hatteras, N.C.) hereafter referred to as the Bight, is characterized as being a homogeneous habitat of relatively flat topography, composed of

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soft sediments, mostly sands, but grading to silt-clay in deeper areas (Stumf and Biggs, 1988; Poppe et al., 1994). Except for relic sand and gravel ridges, exposed Holocene to Pleistocene clay or sandstone in some areas (Allen et al., 1969; Wigley and Theroux, 1981; Stumf and Biggs, 1988; Poppe et al., 1994; NOAA National Data Center-NGDC, 1999), and glacially exposed rock along the southern New England coast, this habitat characterization of the Bight was basically true until European colonization.

Within the last two centuries there has been an increase in hard bottom or reef ("reef" is used hereafter to refer to this multi-dimensional, hard-substrate, structural habitat) habitats in the Bight, which is not commonly recognized by marine geologists and resource managers, e.g. shipwrecks, lost cargos, disposed solid materials, shore-line jetties and groins, submerged pipelines, cables, artificial reefs, and similar objects or material placed in the marine environment by the human population. Some of these human additions are considered objectionable "litter" (Galgani et al., 2000), but larger objects can function as seabed structures that develop and support diverse and special biological communities, even if they can be patchy in distribution. These communities differ significantly from those of the surrounding well surveyed, soft sediment seabed of the Bight.

The expansion of this habitat type in the Bight by man's addition of solid material has probably had an effect on LMR distributions and fisheries (such as American lobster, *Homarus americanus*; cod, *Gadus morhua*; red hake, *Urophycis chuss*; ocean pout, *Macrozoarces americanus*; scup, *Stenotomus chrysops*; black sea bass, *Centropristis striata*; and tautog, *Tautoga onitis*) and possible effect on other resources, but these effects are not well known nor well understood. In fact, reef habitats in general seem underappreciated by northeastern U.S. habitat managers or researchers. For example, no type of reef habitat is even listed as a fishery habitat in recent reviews of northeast fish habitat, except for boulders (Langton et al., 1995; Auster and Langton, 1999), and they are not considered as demersal fish nursery habitat in the Bight (Steves et al., 2000). In the waters south of Cape Hatteras, reef habitats are recognized as important to fisheries and some of the species found in the Middle Atlantic Bight are also part of those fisheries (Miller and Richards, 1979; Parker and Mays, 1998).

ABSTRACT—*One particular habitat type in the Middle Atlantic Bight is not well recognized among fishery scientists and managers, although it is well known and used by recreational and commercial fisheries. This habitat consists of a variety of hard-surface, elevated relief "reef" or reef-like environments that are widely distributed across the predominantly flat or undulating, sandy areas of the Bight and include both natural rocky areas and man-made structures, e.g. shipwrecks and artificial reefs. Although there are natural rock and shellfish reefs in southern New England coastal waters and estuaries throughout the Bight, most reef habitats in the region appear to be man-made, mostly wrecks and "obstructions," and man-made reef habitat modification/creation may be increasing. Very little effort has been devoted to the study of this habitat's dis-tribution, abundance, use by living marine resources and associated biological communities (except on estuarine oyster reefs), and fishery value or management. This poorly studied and surveyed habitat can provide fish refuge from trawls and can be a factor in studies of the distribution and abundance of a variety of reef-associated fishery resources. This review provides a preliminary summary of information found on relative distribution and abundance of reef habitat in the Bight, the living marine resources and biological communities that commonly use it, threats to this habitat and its biological resources, and the value or potential value of artificial reefs to fishery or habitat managers. The purpose of the review is to initiate an awareness among resource managers about this habitat, its role in resource management, and the need for research.*

Although hard bottom habitats off southern New England were explored briefly by naturalist dredge in the latter half of the nineteenth century (Verrill, 1872), submarine canyon and tilefish habitats were examined by submarine (Valentine et al., 1980), and some attention was given to biological fouling (Redfield and Ketchum, 1952), little other work has been done to examine this habitat type in the Bight. Reef habitats in the Bight, although not as wide in occurrence and coverage as the glacially scoured, rocky areas of the Gulf of Maine (Oldale et al., 1973), or the fossil coral rock and live coral patch reefs south of Cape Hatteras (Menzies et al., 1966), may have become common enough to warrant consideration of their role in fishery management in the Bight. Although not as common or as spectacular as in the tropics, reef-like habitats (especially shipwrecks) also support recreational diving in the Bight, and many divers harvest reef fish resources by spear (fish) or hand (lobsters). This recreational diving generates economic benefits to nearby businesses through sales and services.

The introduction of manufactured materials as reef habitat, by both accidental and intentional depositions, is expanding in the Bight. These habitats and their associated biological communities need the ecosystem/community-level attention given similar reef habitats in the adjacent Gulf of Maine and South Atlantic Bight areas (e.g. McCarthy et al., 1979; Hulbert et al., 1982; Wenner et al., 1983; Chester et al., 1984; Sedberry and Van Dolah, 1984; Witman, 1985; Witman and Sebens, 1988; Kirby-Smith, 1989). Man-made or artificial reef habitats are also often suggested as replacement habitats for losses of other habitats, especially in estuaries where in-kind mitigation opportunities are often absent (Sheehy and Vic, 1992; Foster et al., 1994). They are also used to create new habitat, e.g. artificial reefs to enhance fishing or surrounding artificial islands (Williams and Duane, 1975; Seaman and Sprague, 1991), or are segregated as special fishery management areas or reserves (GMFMC, 1999). Because of

these varied roles involving fishery and habitat management, there is need to begin to better understand the community dynamics and fishery value of this habitat type in the Bight.

This paper summarizes available information in four parts:

1) A characterization and preliminary assessment of the abundance and distribution of reef habitats in the Bight;
2) Known or probable fishery resource associations with reef habitats, several species of which are currently considered "overfished" (NMFS, 1999b), including some endangered marine species;
3) What is known of the biological communities that are associated with various estuarine, coastal, and continental shelf reef habitats; and
4) Discusses status and trends in reef habitats, threats to these habitats, some uses of man-made reefs to manage marine resources, and informational or research needs.

This summary is intended to create an awareness of this habitat in the Bight and serve the information needs of habitat and fishery resource managers.

The Middle Atlantic Bight Reefs

The Bight generally is defined to include estuarine and continental shelf waters and seabed between Cape Cod, Mass., and Cape Hatteras, N.C. It is a broad indentation in the coast line between these boundaries with inflections at the mouth of Chesapeake Bay and New York harbor (Fig. 1). Its nonreef benthic environment and associated communities have been reported by Wigley and Theroux (1981) and Theroux and Wigley (1998), and were reviewed by Pacheco (1988), and are characterized as being composed of sediments that range from clay to gravel, with sand being the dominant sediment (Fig. 1). But within this soft sediment matrix, unnoted natural and man-made reef habitats occur in estuaries, along the coast, across the continental shelf, and in deeper waters. A review of these reef habitats and biological associations follows, which in-

cludes references to species, such as aquatic birds, that interact with reef-associated fishes.

Characteristics of Reef Habitats in the Bight

A reef habitat can be composed of natural materials (such as rocks used for shoreline rip rap jetties), sometimes placed by man, or composed of manufactured materials (such as sunken vessels). Some biogenic micro-structures, e.g. coralline algae; anemone, polychaete, or amphipod tubes; or cobble or dead or fossil molluscan shell patches, have some reduced characteristics of a reef habitat. These can support smaller organisms or life stages; Auster et al. (1995) discusses this use of micro-habitat. After a period of submersion and epifaunal colonization, most reef habitats have a similar appearance and function, but there can be subtle differences between natural and man-made reef habitats; the characteristics of each type are reviewed separately. The basic source of information on the distribution of reef habitats is NOAA's NOS Hydrographic Surveys Division Automated Wreck and Obstruction Information System (AWOIS, 1997), although this database only includes structures or reefs that might be of concern to navigation, and many small "reefs" or "snags" are not included in the database. This database is augmented by a summary of artificial reef construction from sources involved in various state artificial reef programs, and a survey of relevant literature. The very abundant and widely distributed shellfish reefs, submerged pipelines, and intertidal man-made structures, e.g. jetties and bulkheads, are only generally considered. No effort is made in this review to estimate the total spatial seabed coverage of all types of reef habitats in the Bight. Some of the targets listed on the maps that seem to be inland are actually within rivers.

Natural reefs

Natural reef habitats in the Bight are found in some areas consisting of biogenic or rock material. Biogenic reefs are created by living stone coral, *Astrangia poculata*, certain shellfishes (east-

ern oyster, *Crassostrea virginica,* and blue mussel, *Mytilus edulis*), and polychaete worms, such as *Sabellaria vulgaris.* These reef-building organisms have been called "physical ecosystem engineers" by Jones et al. (1997) because they add structural complexity (or micro habitats) to environments, which in turn attracts and supports other organisms. Nonbiogenic natural reef habitats are exposed rock outcrops or random boulders left by retreating glaciers or rafted from icebergs, about 12,000 years before present (YBP), or erosion of sediment-covered rock or deltaic deposits of rock, cobble, and gravel along former river channels across a retreating shoreline since the last glacial period. There are reports of submerged ridges of aragonitic sandstones, thought to be relict beach deposits, mid-shelf off Delaware (Allen et al. 1969). Some natural "reefs" can be ephemeral, such as tree trunks that are washed down rivers, become water logged, and sink to the bottom to provide temporary habitat until woodborers gradually degrade them. Collections of dead molluscan shells, such as surf clam, *Spisula solidissima*; and whelks, *Busycon* sp.; and exposed semifossil oyster shell can serve as microreef habitats.

Shellfish reef habitats (primarily oyster and blue mussels) are primarily known to occur in polyhaline estuaries and coastal areas in the Bight, but mussels occur offshore, too. Oyster beds and reefs are found in Chesapeake Bay and its tributaries, Delaware Bay, the Hudson-Raritan Estuary, in coastal areas of Long Island Sound and Southern New England, including bays on Martha's Vineyard (Ford, 1997; MacKenzie, 1997a, b). Oyster beds were more extensive in distribution and abundance in the nineteenth century than currently, and were enhanced in many areas in the 19th and early 20th century by transplanting cultch and spat.

Blue mussel beds are attached to hard surfaces in more marine and cooler coastal waters, (e.g. Steimle and Stone, 1973; Langton et al., 1995; MacKenzie, 1997a). They can also be found adjacent to larger reef structures after being sloughed off by strong currents or storm surges and there they continue to grow and serve as satellite, low-relief reef habitats. Life spans of a decade or less, predation, and harvesting make the presence and size of these beds somewhat dynamic, and they are not usually mapped as reef structures.
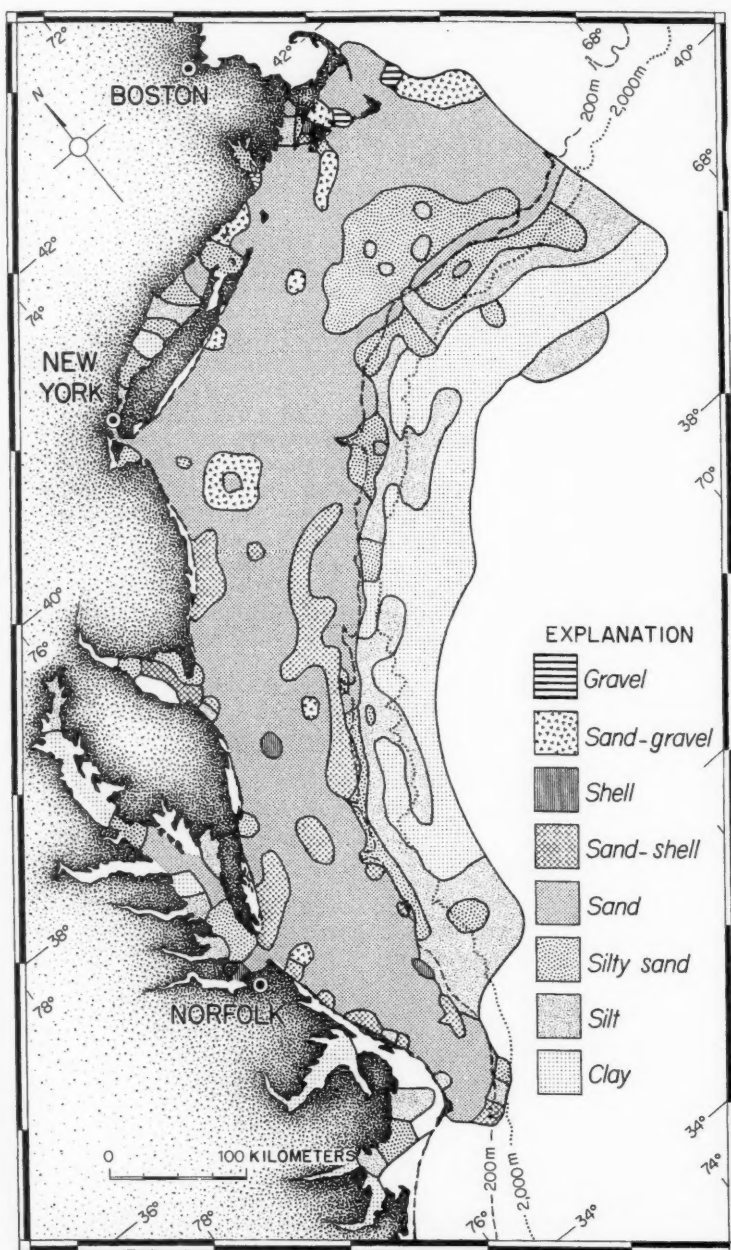

Figure 1.—The underlying dominant sediments types and distributions in the Middle Atlantic Bight (from Wigley and Theroux, 1981).

EXPLANATION

- Gravel
- Sand-gravel
- Shell
- Sand-shell
- Sand
- Silty sand
- Silt
- Clay

Rocky reefs and associated fauna are mostly found in New York Harbor, Long Island Sound, and along the Southern New England coast, and outcrops of glauconitic marl (a soft sedimentary rock) occur off northern New Jersey (the Shrewsbury Rocks and Elberon Grounds). The AWOIS (1997) database represents a rough estimate of reef habitats, including natural rock. For example, there is evidence of aragonitic fossilized sandstone ridges reported off Delaware at about 80 m depth (Allen et al., 1969) that do seem to be in the AWOIS database, and there are "rocky" areas defined by AWOIS at the mouths of Delaware and Chesapeake Bays (Fig. 2) that are not natural, but are protective rip rap. Some natural reef habitat is also known from areas of the outer continental shelf and within submarine canyons where other outcrops of sandstone and clay occur; the exposed clay in this area is further enhanced as fishery habitat by the burrowing activities of tilefish, *Lopholatilus chamaeleonticeps,* and crustaceans, such as American lobster (Cooper et al., 1987; Steimle et al., 1999f), and by soft coral colonization. These deeper reef-like habitats are not included in the AWOIS database nor on Figure 2.

There are anecdotal reports by commercial fishermen of cobbles and loose rock patches associated with gravelly areas in coastal areas, these could represent river deltaic deposits during periods of lower sea levels; but some could be ballast stones from old wooden shipwrecks. Off coastal Delaware and south these rocky patch are also associated with "live bottom," i.e. the rocks are colonized by sea whips, stone coral, and other biogenic structural enhancers (see below).

Man-made reefs

Although native Americans used brush and stone weirs to trap fish in estuaries and rivers, which might be considered a form of artificial habitat which sheltered some fish as well as aggregating them for collection, most man-made contributions to Bight reef habitat have occurred since European colonization in the seventeenth century. As settlers developed the shore-
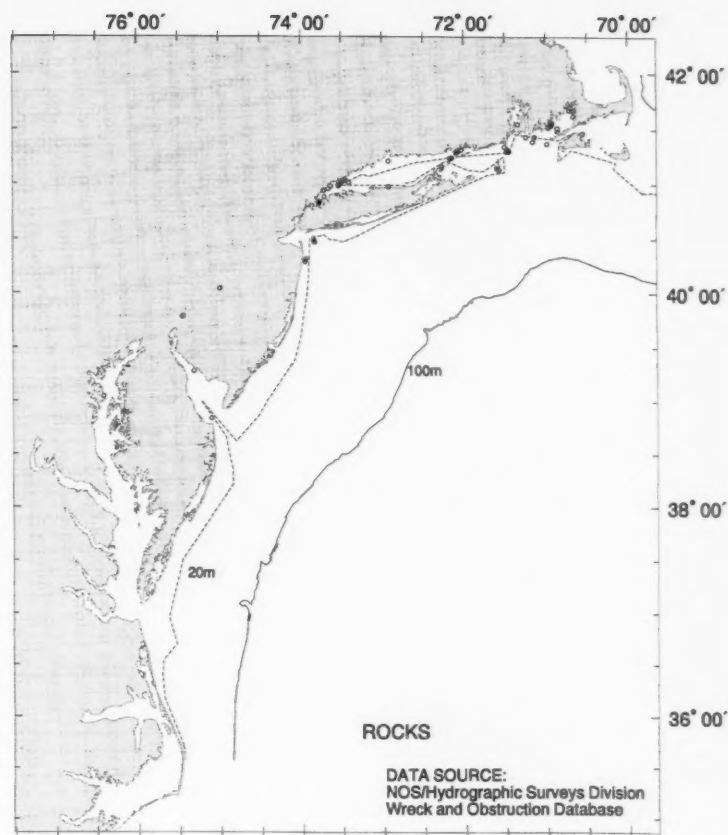

Figure 2.—Distribution of submerged rocky reef areas (O) in the Middle Atlantic Bight, based on NOAA NOS's AWOIS (1997). The targets that appear inland are in the AWOIS database for rivers.

line, they added objects or structures that functioned as reefs to estuaries, coasts, and the shelf by building piers, docks, bulkheads, and leaving wooden shipwrecks. These structures had habitat value similar to submerged trees washed down river into estuarine waters by storms, and in some ways they mitigated the loss of other structured, vegetated habitats (coastal marshes and eel grass beds) that were covered or degraded by shoreline development, although the hard structures did not fully mitigate lost primary productivity. In approximately the last century and a half, metal vessels have gradually replaced large wooden vessels and created more enduring sunken structures. Mid-depth to surface "reef-like" habitat

is also created by epifauna colonizing the system of coastal navigation aids, such as buoys and their anchor chains and the submerged supports of light towers; there are presently no oil or gas rigs in the Bight which would add to this type of habitat. Human activities have introduced rocks, as protective structures (jetties, groins, breakwaters, and ice blockers) along or within most coastal areas or bays, or as former waste material as off the mouth of New York Harbor, i.e. the Subway Rocks, which are material removed while constructing the New York City subway system.

Shipwrecks constitute one of the most abundant types of man-made reef habitat in the Bight. A summary plot of

wrecks from the AWOIS (1997) database suggest that they are most common near the mouths of major estuaries or ports (Fig. 3), as might be expected from the volume of shipping traffic in and out of these ports. However, many smaller or older, partially degraded or buried wrecks are not in the database or shown on these charts, and their distribution is likely to be similar to the plotted shipwrecks. Many of the shipwrecks on the outer continental shelf are products of WW II submarine attacks. As shipwrecks degrade, their structural complexity changes and this affects their habitat value for fishery resources.

Another type of "reef" habitat noted on NOS charts and in the AWOIS (1997) database, is "Obstructions." These are objects on the seabed of unknown composition, and many are probably small or degraded shipwrecks, lost anchors or deck cargo, a few airplane wrecks, and similar objects. The most notable of these are summarized on Figure 4, and, like shipwrecks, the plot focuses on larger targets of potential concern to navigation.

In the last half century or so, fishermen and fishery managers have recognized the value of "reef" and wreck habitats to fisheries, and they have been constructing artificial reefs in coastal waters. The use of artificial reefs for fishery enhancement has continued to expand, although they are a relatively small part of the plotted man-made or overall reef habitat available in the Bight (Fig. 5), in comparison with wrecks and obstructions (Fig. 3, 4). Areas where artificial reefs have been constructed are noted by an older term, "fish havens," on NOS navigation charts but are not included in the AWOIS (1997) database. Artificial reefs placed on the seabed specifically for fishery enhancement tend to be found in coastal and estuarine waters (Fig. 5) and serve primarily the recreational fishery. They have been built and developed in the Bight since the 1920's or 1930's, and especially since the 1960's. Initially they were developed with a variety of recycled materials, ranging from Christmas trees stuck in concrete bases, wooden beer cases half filled with concrete, rubber automobile tires, to the recent use of de-
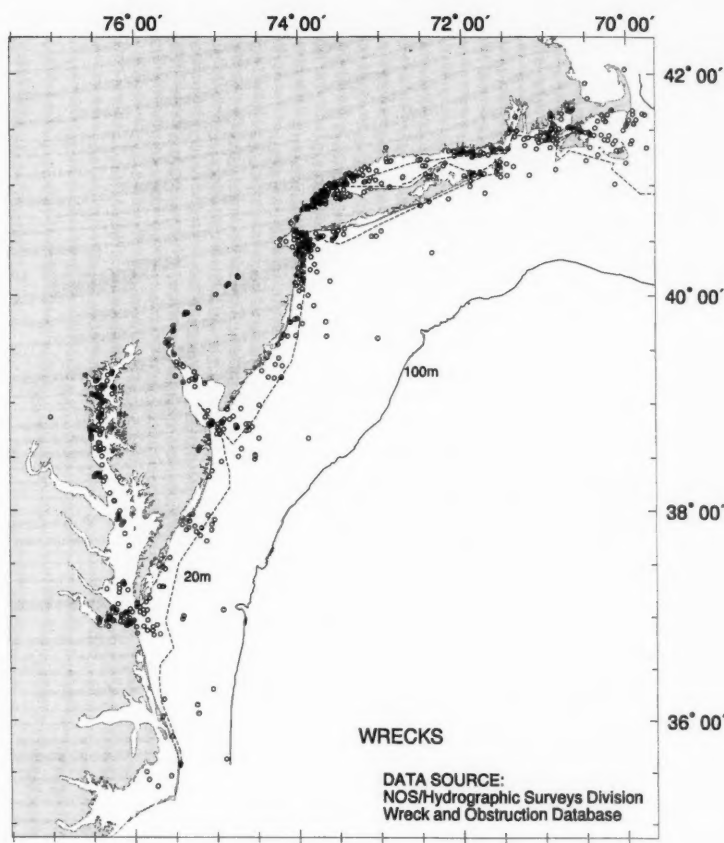

Figure 3.—Distribution of Middle Atlantic Bight shipwrecks (○) in the NOAA NOS's AWOIS (1997) considered to be a concern for navigation. The targets that appear inland are in the AWOIS database for rivers.

militarized combat vehicles and a variety of ships as available at a reasonable cost (Steimle, 1982; Joint Artificial Reef Technical Committee, 1998). In the last decade, prefabricated artificial reef units that are specifically designed and constructed as habitat for fishery resources are increasingly being deployed (Sheehy and Vic, 1992). The contribution of artificial reefs to reef-fish productivity has been controversial and the debate continues and fish or fishery productivity may vary among reef locality and other factors (American Fisheries Society, 1997).

A summary of all reef or reef-like habitats, i.e. Fig. 2–5, is shown on Fig. 6, which should be considered a minimum estimate of the distribution and relative

abundance of this habitat in the Bight, because of the reasons previously mentioned. The term, "non-biogenic" is used on this figure to note that live coral, mussels, and oyster beds/reefs are not included.

The concept of a reef habitat is more complex than being either natural or man-made and involves a variety of conditions under which a reef or reef-like conditions exists in the Bight. Some characteristics of different reef or reef-like habitats found in the Bight are summarized in Table 1.

Reef-associated Fishery Resources in the Bight

Reef habitats of all types within the Bight are used by a wide variety of fish-

ery resources (Hildebrand and Schroeder, 1928; Bigelow and Schroeder, 1953) and a few threatened or endangered species (Lutz and Musick, 1996). Table 2 summarizes most of these species and notes their known or suspected reef habitat associations; however, it should be noted that very little information is available on the invertebrate or fish fauna on reef habitats in the Bight, especially in relatively deep (>30 m) waters.

Although many fishery species are closely associated with reef habitats, the reef may not adequately supply all of their needs, especially food, and the availability of non-reef resources can be important to these species. For example, black sea bass, which is a common reef habitat-associated fish mostly found during the warmer months in the Bight, may obtain much of its food from the sandy bottom or water column around a coastal artificial reef habitat (Steimle and Figley, 1996). Thus, the near-reef, open bottom/water habitat and its biological resources are linked to the fishery resource production function of a reef habitat. The open sandy bottom fauna near reef habitat, conversely, can be affected by the presence of a reef and its predatory fauna.

The habitat needs of reef-associated fishery resources often shift during ontogenetic development. Many reef species use the marine water column as larvae, estuarine structures as juveniles, and gradually return to deeper and more marine habitats at the end of their first season. In the Bight there can also be a seasonal shift in habitat use among subadults and adults of certain species, i.e. winter and summer habitat use can also differ significantly (Steimle et al., 1999 b–f; Steimle and Shaheen, 1999; NMFS, 1999a).

Other Potential or Transient Reef-associated LMR's in the Bight

Some reef associated taxa or species, that are not included in Table 2 and are not presently considered a "living resource" in a fishery management sense, might be of greater value in the future, e.g. for biomedical-pharmaceutical research and industry (Faulkner, 1984). Reef-associated taxa known to have
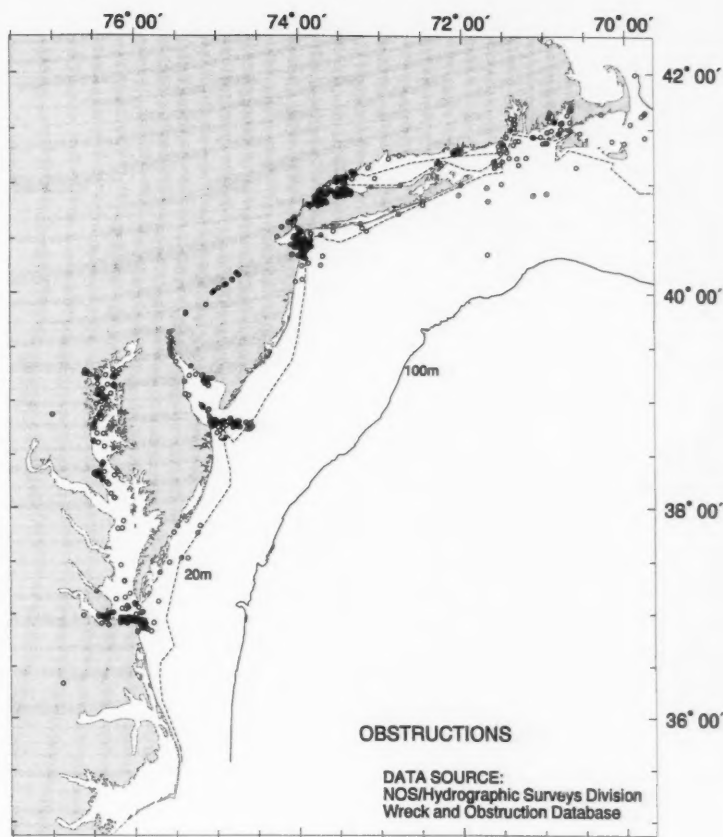

Figure 4.—Distribution of "obstructions" (O) in the NOAA NOS navigational chart database. The targets that appear inland are in the AWOIS database for rivers.

Table 1.—Summary of physical and biological characteristics of natural and man-made reef or reef-like habitats in the Middle Atlantic Bight.

Natural: These are submerged rocks and other hard materials or solid structures made by living organisms (biogenic materials).

Estuarine: Reefs in this environment consist of oysters, mussel, sponge, and tube worm beds: exposed stiff clay, peat, or rocky outcrops; waterlogged trees; or boulder or cobble fields. Oyster and mussels are fishery resource species in their own right, and these estuarine biogenic and non-biogenic habitats provide shelter and food for a variety of juvenile to adult fish (see below).

Coastal (< 12 miles): Mussel and stone coral beds form biogenic reefs here, and other reefs consist of rocky outcrops, such as soft marl off northern N.J. and harder rock from N.Y. Harbor east along the southern New England coast (Fig. 2); glacial erratic boulders or cobble accumulations from eastern Long Island to Cape Cod with other submerged cobble/ gravel banks reported off New Jersey, Delaware, and Maryland[1]; relict shell fields; exposed stiff clay or peat deposits; and kelp beds are found along southern New England.

Shelf: Reef habitats are scarcer in deeper water but glacial erratic boulders; exposed rock or stiff clay at or near the edge of the continental shelf or at the shelf edge heads of submarine canyons; relict clay or peat deposits; and shell fields provide patches or bands of reef-like habitat.

Man-made: These types of structured habitats have been available since the 17th century, and a good part of this habitat is from shoreline construction, such as piers and jetties, but also include the remains of shipwrecks and various materials deposited to provide an artificial reef-type habitat, as per Fig. 3-5.

Estuarine: This type of habitat is often formed by shoreline development, including functional and decaying bulkheads, bridge abutements, piers and docks, protective rip rap, groins and jetties; navigational aids such as lighthouses and buoys; clay or rock exposed by dredging; submerged natural gas, storm water, processed sewage effluent pipelines; exposed communication cables; sunk or abandoned vessels (including ballast rock piles); and other small to medium sized materials ranging from beverage containers to vehicles; waterlogged timber; and artificial reefs build of various reused and some specifically designed materials to support shell- and finfisheries.

Coastal (< 12 miles) and Shelf: Man-made structured habitats in this broad marine zone consist of basically many of the same materials or structures as are found in estuaries, although some structures are larger in size, e.g. shipwrecks and artificial reefs, but can include lost ship cargos, and exposed exploratory oil and gas pipe heads in deeper waters.

[1] Monty Hawkins, partyboat captain, Ocean City Md, personal commun., 2000.
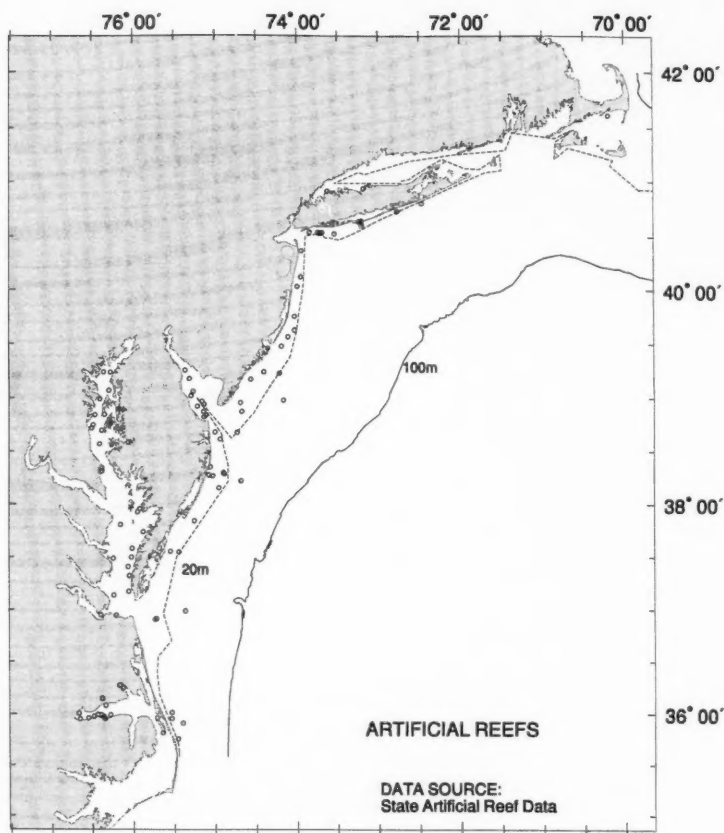
Figure 5.—Distribution of artificial reefs, or fish havens, (○) in the Middle Atlantic Bight, based on individual state artificial reef program data.

such potential qualities include: algae species, sponges, coelenterates, nudibranch mollusks, and tunicates (Lustigman et al., 1992).

Other fishery resources commonly caught or observed above or near high profile reef habitats are bluefish, *Pomatomus saltatrix*; mackerels and tunas, Scombridae; jacks, Carangidae; and some benthic species such as summer flounder, *Paralichthys dentata*. These fish predators take advantage of aggregations of prey on the reef or may be behaviorally attracted to the reef structure or the flow refuge effects of structure (Westman, 1958; Figley, 1996).

The fish that frequent reef habitats are often less subject to commercial fishing pressure, because the relatively high relief and complex structure of

many reefs inhibit the use of towed fishing gear, or the reefs provide shelter when this gear passes over a low profile structure; however, lobster and fish traps and gill nets are often effective on or near reefs. Most reefs are heavily used by recreational fishermen and divers.

Reef Communities in the Bight

Reef habitats support biological communities (used here to mean organisms that are commonly found together with some degree of interaction) that are dependent upon or which significantly benefit from this habitat type. These communities range from microscopic algae and large kelp (in cooler waters) growing on reef surfaces to fishes and possibly sea turtles (Chelo-

niidae). Below is an overview of the communities known to be commonly found on subtidal reef structures in the Bight. The type of reef surface, i.e. rock, wood, metal, or other, has a variable effect on the community formed on that surface, but this effect is only briefly discussed here because of the limited available information. Intertidal, semi-hard surface communities (e.g. peat banks) and submerged aquatic vegetation also provide some of the habitat characteristics of reefs, and these functions are becoming better known (Able et al., 1988) and are also not discussed here. Ducks and other vertebrates are included in the habitat use synopsis below, when appropriate, as a reminder of their possible predatory or competitive interactions with reef fish and other reef-associated LMR's. Scientific names are included only for species not found in Table 2.

Estuarine Reef Communities

Epibenthic and Epibiotic (Organisms Attached to Reef or Shellfish Surfaces)

Several types of polyhaline estuarine reef epibenthic communities exist in the Bight. These communities include oyster beds; blue mussel beds; communities attached to nonbiogenic hard surfaces such as rock, wood, and metal; and those using semi-hard surfaces such as stiff clay and peat.

Oyster reefs The shells of oysters support a diverse epibiotic community that can include barnacles, *Balanus* sp.; ribbed mussels, *Geukensia demissa*; and blue mussels depending on salinity, algae, sponge, tube worms (*Spirobis* sp., *Polydora* sp., and other species), anemones, hydroids (*Obelia* sp. and other species), bryozoa (*Membranipora* sp. and other species), and other taxa (Watling and Maurer, 1972; Maurer and Watling, 1973; Kinner and Maurer, 1977; Larsen, 1985; Zimmerman et al., 1989, Coen et al., 1999). Silt accumulated between the oyster shells can support benthic invertebrates that are also found on the soft bottoms of the area.

Blue mussel beds Many organisms are found epibiotically on mussel shells; these can include many of the same epi-

biotic organisms found on oyster beds: barnacles, algae, sponge, the same types of tube worms, hydroids, anemones, bryozoa, and slipper shells *Crepidula* sp.(Kinner and Maurer, 1977; Newell, 1989). Additional, nonepibiotic macrofauna (mainly a diversity of polychaetes and amphipods) also benefit from the mussels and live within the interstitial spaces among the mussel shells and byssus threads.

Other hard surfaces (including a diversity of natural and man-made submerged materials) These surfaces, like that of oysters and mussels, can support algae where light is sufficient, barnacles, sponge, tube worms (including *Sabellaria vulgaris* and others), hydroids, anemones, encrusting bryozoans, oysters, blue mussels, the jingle shell *Anomia* sp., northern stone coral, *Astrangia poculata* (in more marine waters), sea whips *Leptogorgia* sp. (in Chesapeake Bay), tunicates *Molgula* sp., and caprellid amphipods (Maloney, 1958; Westman, 1958; Watling and Maurer, 1972; Dean, 1977; Otsuka and Dauer, 1982). Wooden structures within estuaries can also be infested with destructive borers such as *Teredo navalis*, and gribbles, *Limnoria lignorum* (Nigrelli and Ricciuti, 1970) and weathered creosoted or other antiborer-treated pilings can become substrates for some epifaunal colonization, even though borers and others may be temporarily inhibited by the chemical treatment (Stewart, 1983).

Semi-hard clay and Spartina peat "reefs" These softer surfaces can support burrowing mollusks (piddocks such as *Pholus* sp., *Cyrtopleura costata, Barnea truncata, Zirfaea crispata*) and epibenthic algae (Able et al., 1988); motile organisms, such as juvenile American lobsters and American eels, also occur in this habitat and are discussed below.

Of note and potential interest to fish recruitment success is that the larvae of certain epibenthic (reef) organisms can be very abundant at times in the meroplankton, e.g. barnacle cyprids and mussel larvae, and be a significant source of planktonic food for some larval fishery resources (Richards, 1963).
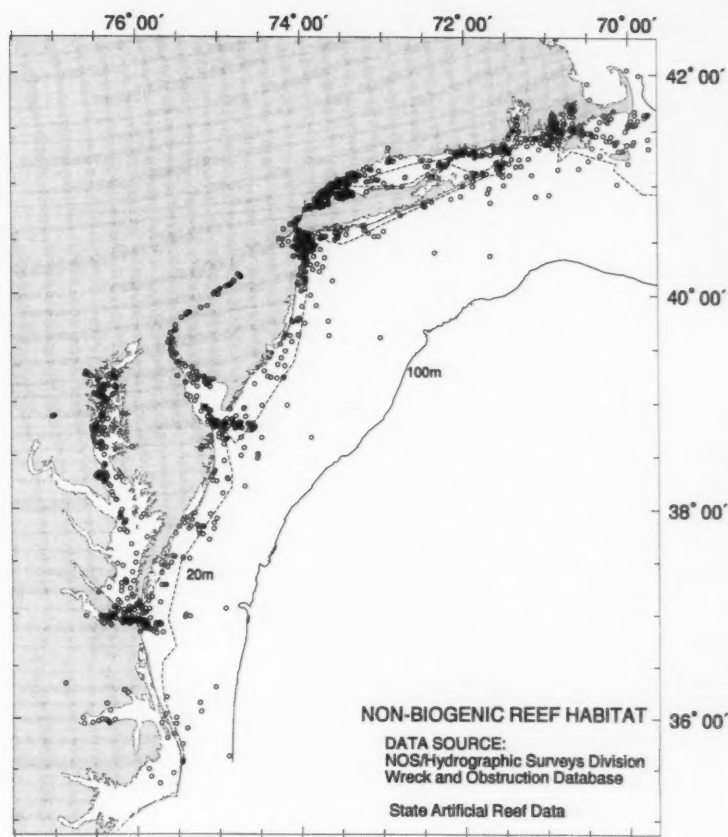
Figure 6.—Summary of all reef habitats (except biogenic, such as mussel or oyster beds) (○), Figs. 2-5, in the Middle Atlantic Bight. The targets that appear inland are in the AWOIS database for rivers.

Motile Epibenthic Invertebrates

These mostly include decapod crustaceans, such as mud (xanthid) crabs; blue crabs, *Callinectes sapidus*; rock crabs; spider crabs, *Libinia emarginata*; and juvenile American lobsters (although this species is scarce south of Delaware Bay, except in deeper waters), and sea stars, *Asterias* sp. and *Henricia* sp. (Jeffries, 1966; Briggs, 1975; Leathem and Maurer, 1980; Able et al., 1988; Barshaw et al., 1994; Wilk et al., 1998).

Fish

A number of fishes are commonly or seasonally found on estuarine reef or reef-like estuarine habitats. They include adults and juveniles, and species that can be prey (e.g. gobies, *Gobisoma* sp.), predators (e.g. toadfish, *Opsanus tau*), or competitors (e.g. cunner) with resource species (Breitburg, 1999). There is a gradual shift in the fish species assemblages that are commonly associated with reef habitats from the warmer waters off Virginia to the cooler waters off southern Massachusetts, and they are thus discussed by subregions.

Chesapeake Bight (Delaware–North Carolina) Gobies, spot, striped bass, black sea bass, white perch, *Morone americanus*; toadfish, scup, drum, croaker, spot, sheepshead porgy, pinfish, tautog, and northern puffer, *Sphaeroides maculatus*; have been reported common on reef habitats in this area

Table 2.—List of fishery species that are commonly found on reef or reef-like habitats in the Middle Atlantic Bight.

Species	Life stage/reef habitat use	Notes
Algae (kelp, *Laminaria* sp., dulse, etc.)	All stage grow attached to estuarine/marine hard surfaces.	Grows on inter/subtidal surfaces along southern New England coast as deep as light penetration allow and provides shelter; some are harvested.
Invertebrates **Mollusks** Blue mussel *Mytilus edilis*	All stages grow attached to hard surfaces in polyhaline-marine waters.	Colonizes intertidal/subtidal surfaces but becomes scarcer towards N.C.; important prey for many reef fishery resources; harvested as adults; increases habitat structural complexity and biodiversity.
Eastern oyster *Crassostrea virginica*	All stages grow attached to hard surfaces in polyhaline-estuarine waters.	Colonizes hard surfaces and/or creates low profile reefs; harvested as juveniles (spat for transplanting) and adults; increases habitat structural complexity and biodiversity.
Longfin squid *Loligo pealei*	Eggs are attached to hard objects in marine waters.	Hard surfaces of all sizes seem important for egg mass attachment. Eggs and larvae can be prey.
Crustaceans American lobster *Homarus americanus*	All post-larval stages use shelter in polyhaline-marine waters.	Lobsters are common reef habitat dwellers but are less common south of Delaware Bay; maintain reef habitat structural complexity by clearing burrows.
Jonah crab *Cancer borealis*	All post-larval stages use shelter in polyhaline-marine waters.	This larger crab is common to reef habitats; claws are harvested.
Rock crab *Cancer irroratus*	All post-larval stages use shelter in polyhaline-marine waters.	Common on reef habitats as well as on most other habitats; juveniles or smaller sizes important prey for fish and lobsters; claws are harvested.
Fish American eel *Anguilla rostrata*	Adults found in estuarine to coastal marine reefs as well as elsewhere.	This eel is found seasonally in estuarine areas, including holes in peat banks; harvested by trap and by recreational fishery.
Conger eel *Conger oceanicus*	Juveniles and adults common in polyhaline-marine structures.	This larger eel preys on smaller reef fish; hard to catch but desirable.
Atlantic cod *Gadus morhua*	Juveniles and adults common on polyhaline-marine reefs.	This species feeds on reef organisms; uses structure for shelter; but only found during cooler seasons south of Long Island, N.Y. to about Delaware.
Pollack *Pollachius virens*	Juveniles and adults common on polyhaline-marine reefs.	Uses structure for shelter or for feeding; but only found during cooler seasons south of Long Island, N.Y. to about Delaware.
Red hake *Urophycis chuss*	Juveniles and adults common on polyhaline-marine reefs.	Common reef habitat dweller; preys on small crabs and other organisms found on or near reefs; commercially and recreationally harvested.
Striped bass *Morone saxitilus*	Juveniles and adults common on estuarine and coastal reefs.	Juveniles use estuarine structures for shelter; adults find prey near estuarine and coastal structures.
Black sea bass *Centropristis striata*	Juveniles and adults common on estuarine and coastal reefs.	Juveniles use estuarine and coastal structures, and adults mostly use coastal and midshelf structures during warmer seasons.
Gag grouper *Mycteroperca microlepis*	Juveniles and adults common on southern Bight reef habitats.	Important but variably available fishery species off Virginia and North Carolina.
Scup (porgy) *Stenotomus chrysops*	Juveniles and adults common on estuarine and coastal reefs.	Small schools of this species visit coastal reefs for prey and shelter during warmer seasons; found offshore and to the south in the winter.
Spot *Leiostomus xanthurus*	Juveniles and adults common on estuarine and coastal reefs.	A warm season user of reef habitats north on Chesapeake Bay.
Sheepshead (porgy) *Archosargus probatocephalus*	Juveniles and adults common on southern Bight reef habitats.	Common on estuarine (including oyster beds) and coastal reefs, mostly south of Delaware Bay.
Atlantic croaker *Micropogonias undulatus*	Juveniles and adults common on estuarine and coastal reefs.	Common on estuarine (including oyster beds) and coastal reefs, mostly south of Delaware Bay.
Black drum *Pogonias cromis*	Juveniles and adults common on estuarine and coastal reefs.	Common on estuarine (including oyster beds) and coastal reefs, mostly south of Delaware Bay.
Tilefish *Lopholatilus chamaeleonticeps*	Juveniles /adults use rocky areas or holes in stiff clay at the edge of continental shelf and upper slope.	This species contributes to the creation and persistence of the rough bottom habitat and associated biological community found in certain areas of the outer shelf and upper slope.
Cunner *Tautogolabrus adspersus*	All post-larval stages are associated with marine-polyhaline reef habitats.	A very common small reef fish, especially in the northern Bight; prey for other fish found on or visiting reefs. Hibernates on reefs in cold winters.
Tautog *Tautoga onitis*	All post-larval stages are associated with marine-polyhaline reef habitats.	A common larger reef fish that prey heavily upon mussels; youngest juvenile found in estuaries; may hibernate during cold winters off New England.
Gray triggerfish *Balistes capriscus*	Juveniles/adults are warm-season reef dwellers.	Found on marine reefs and preys on reef dwellers; growing in popularity as food fish.
Ocean pout *Macrozoarces americanus*	All life stages found on reef habitat, including eggs which are nested.	Adults make and possibly guard egg nests within reef structures during the winter.
Reptilia Sea turtles *Eucheloniodea*	Juveniles and adults of several species are associated with reefs.	Sea turtles are common summer visitors to the Bight and are known to use reef structures as sheltered resting areas and can prey on reef crabs.
Mammalia Harbor seal *Phoca vitulina*	Juveniles and adults use the above water parts of reefs as resting areas.	Harbor seals are winter visitors to the northern Bight and are commonly observed on dry parts of submerged structures and may prey on associated reef fish.
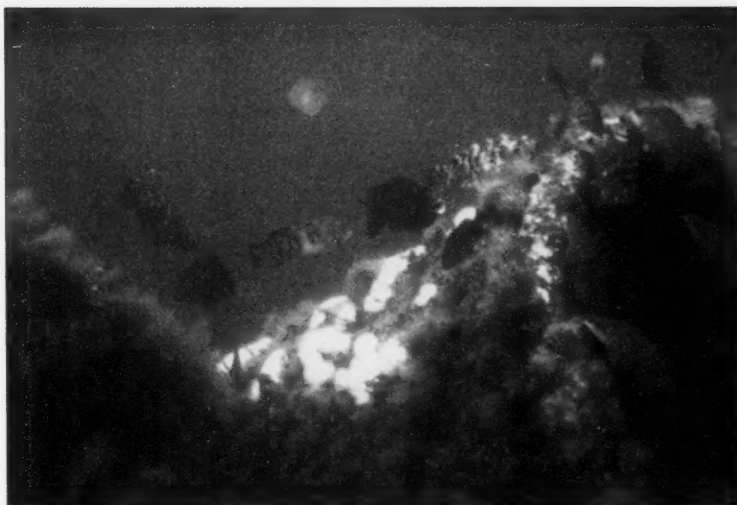
An assemblage of resident Tautog, *Tautoga onitis*, and cunner, *Tautogolabrus adspersus*, on some concrete pipe artificial reef material off New York. Photographer: Christopher J. LaPorta.

Tautog are common at the interface between the predominant open sandy bottom of the Middle Atlantic Bight and reef-like structures. Photographer: Christopher J. LaPorta.

A tautog, *Tautoga onitis*, that sometimes seeks shellfish prey on nearby sandy habitats, always returns to a reef structure.

(Arve, 1960; Richards and Castagna, 1970; Feigenbaum et al., 1985; Breitburg, 1999; Coen et al., 1999).

New York Bight (New Jersey–southern Long Island, N.Y.) Cunner, toadfish, spot, gobies, striped bass, sculpins, juvenile Atlantic cod, juvenile tautog, black sea bass, scup, rock gunnel, *Pholis gunnellus;* conger eel, American eel, red hake, and northern puffer have been reported on reef habitats in estuaries of this area (Briggs, 1975; Auster, 1989; Able et al., 1998).

Southern New England (Long Island Sound–Cape Cod) Cunner, toadfish, striped bass, scup, tautog, black sea bass, rock gunnel, conger eel, Ameri-can eel, ocean pout, red hake, white hake, cod, juvenile pollack, and various nonfishery species have been reported on mostly rocky estuarine reefs in this area (Nichols and Breder, 1927; Able et al., 1988).

Other Vertebrates (Diving birds, seals)

Several species of diving ducks and geese (Anatidae) feed seasonally upon submerged algae, mussels, and other organisms growing upon shallow reef habitats, e.g. brant, *Branta branta*; scaup, *Aythya* sp.; goldeneye, *Bucephala* sp., scoters, *Melanitta* sp., old squaw, *Clangula hyemalis*; eiders, *Somateria* sp.; and Harlequin ducks, *Histrionicus* *histrionicus*; other species can feed on small fish they find on shallow reefs, e.g. wintering loons,*Gavia* sp.; and mergansers, *Mergus* sp.; and cormorants, *Phalacrocorax* sp.; most of the year (Martin et al., 1951). In the winter, harbor seals, *Phoca vitulina,* visit the Bight, to at least New Jersey, and may find prey around reef habitats near their haul out, resting places.

Coastal (to depths of ~25 m)

Epibenthic

Exposed rock–soft marl (e.g. Shrewsbury Rocks off northern N.J.) Certain boring mollusks (piddocks such as *Cyr-*

Sea anemones, *Metridium senile*, and other epifauna that are typical of a well-established hard surface epifauna community in the Middle Atlantic Bight. Photographer: Christopher J. LaPorta.

White frilly patches of northern stone coral, *Astrangia poculanta*; anemones, *Metridium senile*; and various hydroids often dominate reef habitat epifaunal communities, when blue mussels, *Mytilus edulis*, are absent. Photographer: Christopher J. LaPorta.
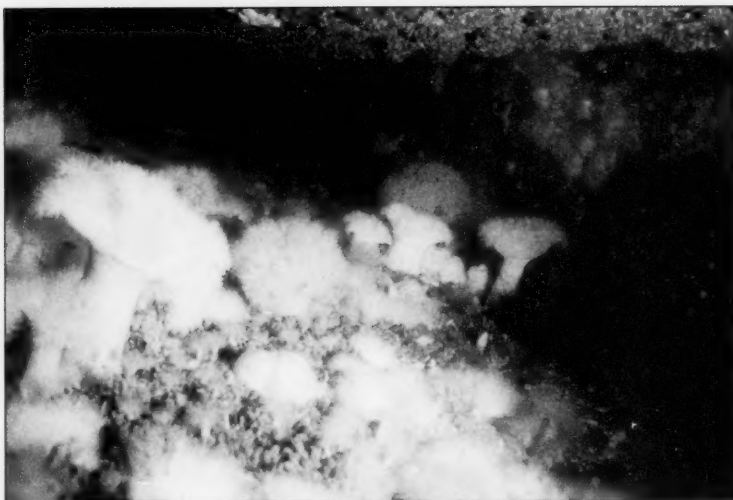
Dense epifaunal growth on exposed hard structure or rocks provides abundant opportunities for juvenile or large fishery resources to find shelter.
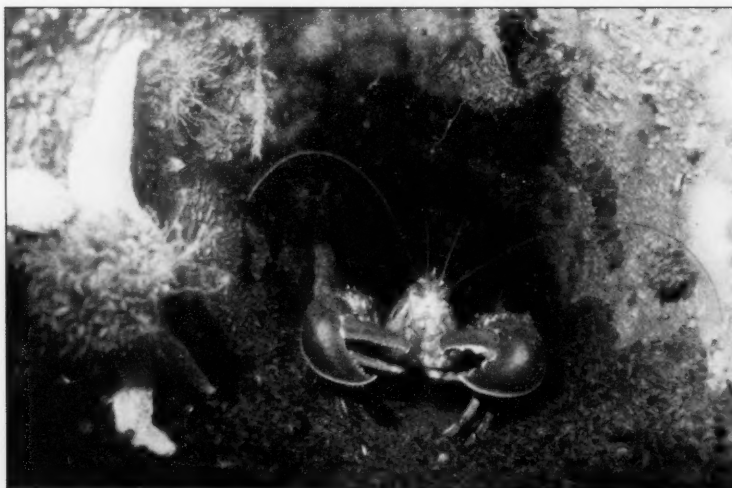
Small American lobsters, *Homarus americanus*, are common within the shelter provided by reef habitats in the Middle Atlantic Bight, and come out at night to feed on or near this habitat. Photographer: Christopher J. LaPorta.
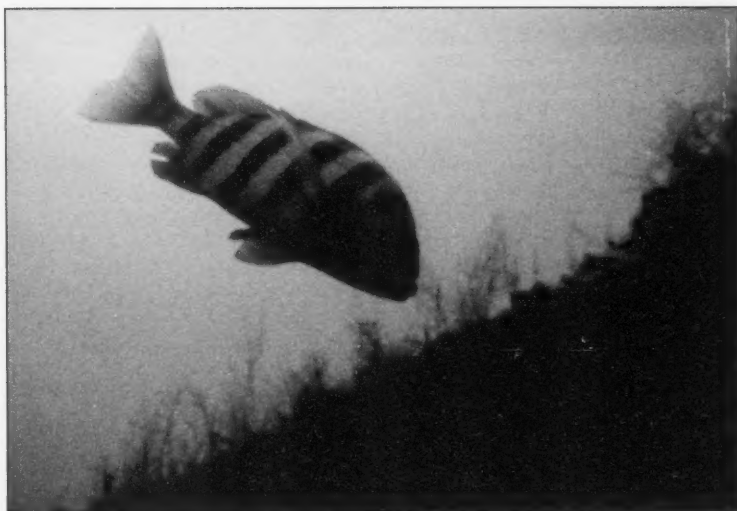
In the southern Middle Atlantic Bight large sheepshead porgy, *Archosargus probatocephalus*, are common residents of reef structures and feed on epifauna.

Juvenile and adult cunner, *Tautogolabrus adspersus*, are permanent residents of reef habitats in the Middle Atlantic Bight. Photographer: Christopher J. LaPorta.

Blue mussels, *Mytilus edulis*, commonly dominate the epifaunal community on reef structures in the Middle Atlantic Bight and are readily eaten by a variety of fish and crustacean shellfish, including the cunner, *Tautogolabrus adspersus*, that is present in this photo.

topleura costata and *Zirfaea crispata*) add complexity as they gradually degrade this substrate. The epifauna on this substrate also includes that noted below for harder substrate (Westman, 1958).

Harder rock When available, this rock can be colonized by red algae (*Phyllophora* sp.); sponges such as *Halichondria* sp. and *Polymastia* sp.; large

anemones (*Metridium senile*, *Tealia* sp., or *Stomphia careola*); various hydroids (*Tubularia* sp., *Obelia* sp., *Campanularis* sp.); northern stone coral, soft coral (*Alcyonaria* sp.) off New England, and sea whips (*Leptogorgia* sp.) south of New Jersey where it becomes part of a "live bottom" community that is most common south of Virginia; barnacles; blue mussels, horse mussels *Modiolus*

modiolus in deeper and cooler waters off southern New England; the jingle shell *Anomia simplex*; bryozoans, including *Bugula* sp.; skeleton (caprellid) and tubiculous amphipods, such as *Jassa falcata*; and tubiculous polychaetes, such as *Sabellaria vulgaris* and *Hydroides dianthus*. Much hard rock reef structure has been added to the shoreline of the Bight in the form of

jetties, groins, rip rap, and groins that abut the shoreline as beach and other protection; these can support less stabile communities because of the greater environmental extremes and stresses that occur in this littoral zone, although fishery resources frequent them when the rocks are covered by water.

Wrecks and artificial reefs (of various compositions) Wood: When exposed, this provides a substrate similar to soft rock, but can include wood borers (e.g. *Teredo* sp. and *Xylophaga atlantica*) that also degrade this type of reef material, which is why they do not usually persist as significant three-dimensional structures or habitat for more that a few decades, unless periodically covered and protected by sediment.

Metal: As per hard rock, but the tendency of sheets of rust to slough off the wreck surface creates a less stabile community; these surfaces are often colonized by hydroids, like *Tubularia crocea*; anemones, mostly *Metridium senile*; northern stone coral; blue mussels; barnacles; sea stars; and related fauna (Bulloch, 1965; Feigenbaum et al., 1985: Chee[1]).

Kelp Laminaria sp. beds occur in Long Island Sound and north and are noted separately from the seaweeds listed elsewhere. Kelp grows only on hard reef-like surfaces and adds vertical relief and more complexity to reef habitats, as well as contributing to primary and detrital production (Alfieri, 1975).

Other materials (such as various plastics and synthetic materials, such as rubber and concrete) These epibenthic communities can be similar to that found on rock and metal reefs (Alfieri, 1975; McCullough, 1975; Woodhead and Jacobson, 1985; Figley, 1989).

Motile invertebrates

American lobsters, rock crabs, Jonah crabs, spider crabs, sea stars, and urchins, *Arbacia punctulata*, are found on these reefs (Westman, 1958; Cobb, 1971; Briggs and Zawacki, 1974; Briggs, 1975; Alfieri, 1975; Sheehy, 1976; Fei-

genbaum et al., 1985; Lavalli and Barshaw, 1986; Karnofsky et al., 1989a, b; Figley and Dixon, 1994; Mercaldo-Allen and Kuropat, 1994; Chee[1]). Mass aggregations of Jonah and rock crabs were reported on Southern New England rocky ledges (Auster and DeGoursey, 1983). *Loligo* squid usually attach their egg clusters to a hard object, such as a reef surface, or shells, gravel, or other hard surfaces on the seabed (Griswold and Prezioso, 1981; Roper et al., 1984).

Fish

Chesapeake Bight Black sea bass, pinfish, *Lagodon rhomboides*; scup, cunner, red hake, gray triggerfish, black grouper, *Mycteroperca bonaci*; smooth dogfish, *Mustelus canis*; summer flounder, scads, *Decapterus* sp.; bluefish, and amberjack, *Seriola dumerili*, have been reported as common over these reefs (Feigenbaum et al., 1985; Chee[1]).

New York Bight Atlantic cod, gray trigger fish, scup, black sea bass, tautog, ocean pout, red hake, conger eel, cunner, sea raven, *Hemitripterus americanus*; and rock gunnel have been reported on reefs in this area (Westman, 1958; Briggs, 1975; Steimle and Ogren, 1982; Woodhead et al., 1985; Figley and Dixon, 1994).

Southern New England Scup, black sea bass, tautog, Atlantic cod, ocean pout, red hake, conger eel, cunner, sea raven, and radiated shanny, *Ulvaria subbifurcata*, have been reported on these reefs (Alfieri, 1975; Carr and Amaral, 1981).

Other Vertebrates (Diving birds, seals)

These use shallow coastal or shoreline reefs, e.g. jetties, as per estuarine reefs, above.

Shelf (generally depths >25 m)

Epibenthic

Rocks and boulders Few rocky ledges are found on the Bight's continental shelf (these occur off southern New England), and most rocky habitat consists of boulder and cobble residue from periods when glaciers covered New England and icebergs drifted in the Bight, the last glacial period being about 12,000 YBP. Reports of the epifauna in this Bight substrate include

most of the species noted in the above Coastal section. The epifaunal colonization of the exposed outer shelf sandstone ridges, reported by Allen et al. (1969), is unreported.

Wrecks and artificial reefs Size, composition, location, and age affect the structure and habitat value of these reefs. These factors also affect the habitat value of artificial reefs that were specifically constructed to support fishing. Few scientific studies are known of the epibenthic fauna of wrecks and artificial reefs on the Bight shelf, and those that are known are mostly within the coastal zone (Figley, 1989; Figley and Dixon, 1994); or are not quantitative or are anecdotal (Bulloch, 1965).

Other solid substrates Exposed submarine communication cables can be colonized by borers and epifauna (Snoke, 1957), and can serve as limited reef habitat for organisms of suitable size.

Motile Invertebrates

Most of the motile organisms noted above for the coastal areas are also commonly found on the shelf, although at the shelf edge, some deepwater taxa occur (Cooper and Uzmann, 1971; Wigley and Theroux, 1981; Theroux and Wigley, 1998).

Fish

Chesapeake Bight Reef fish include resident species (black sea bass, scup, tautog, and cunner), seasonal residents (gag, sheepshead porgy, round herring, and sardines), or transients (amberjack, spadefish, gray triggerfish, various mackerels and small tunas, and the spot-tailed pinfish, *Diplodus holbrooki*) (Eklund and Targett, 1991; Adams, 1993).

New York Bight Gray triggerfish, scup, black sea bass, tautog, Atlantic cod, ocean pout, red hake, conger eel, cunner, sea raven, rock gunnel, pollack, and white hake have been commonly reported on these deeper reefs (Bulloch, 1965; Woodhead et al., 1985).

Southern New England Scup, black sea bass, tautog, Atlantic cod, ocean pout, red hake, conger eel, and cunner occur here (Auster, 1984), as well as other species that are found in the New York Bight.

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[1]Chee, P. K. 1976. The ichthyofauna of the Chesapeake Light Tower. Old Dominion Univ., Norfolk, Va., Unpubl. Rep., 26 p.

Outer shelf reefs and clay burrows (and the "pueblo village community" along southern Georges Bank) Tilefish, white hake, and conger eel are reported using this habitat, as well as smaller species (Valentine et al., 1980; Cooper et al., 1987).

Other Vertebrates

This habitat is too deep for those bird or seal species that could use estuarine and coastal reefs.

Significance, Status, and Trends of Bight Reef Habitats and LMR's

The reef habitats in the Bight are significant to fisheries because they expand the range of some reef-associated species and perhaps their population abundance, possibly beyond the apparent extent of seabed area the reefs cover, as per Figure 6. The growing array or network of reef habitats (all types), that occur or have become established or specifically placed along the coast and across the shelf, can also provide corridors of supporting habitat for some reef-associated species, such as black sea bass, to use during seasonal migrations (Fig. 6). As more fine-scale, side-scan sonar seabed mapping becomes available, more low profile hard bottom and reefs will undoubtedly become known or identified, including many of the objects classified as "obstructions" by NOS or known as "snags" by fishermen. Table 2 shows that a variety of important commercial and recreational fishery resources are known to be associated or depend on reef habitats for some or most of their life history, and reef structures can serve as refuges from trawling for some species. Certain commercial fisheries, such as American lobster or fish trapping and gill netting, favor reef habitats, and recreational fishermen have long valued wrecks and reefs as fishing grounds. It is also becoming evident that several forms of estuarine and coastal reef habitats serve as juvenile fish nurseries in the Bight, e.g. oyster and mussel beds, and artificial reefs can increase this function (Heise and Bortone, 1999).

Natural reef habitats occur primarily in the Bight from within and just outside New York Harbor, through Long Island Sound, and along the Southern New England coast, and may be fairly static, although some rock reefs have been removed or reduced because of their hazard to deep-draft ship navigation, or been covered by shoreline development or silt. The reports of sandstone outcrops on the continental shelf off New Jersey and Maryland need further investigation as to their significance as fishery habitat. Oyster reef habitats in many estuaries are greatly reduced, especially since the 1950's (MacKenzie, 1997a, b). Made-man "reefs" of all sizes are continuing to add this type of habitat to the environment in all areas via accidental, careless, and intentional means. South of Long Island Sound, man-made reef habitats probably contribute significantly to the wider distribution of reef-associated species.

Although there have been studies of epibenthic fouling (Maloney, 1958) and fishery use of reef habitats in the Bight (Figley, 1996), reef habitats in this area have not been well studied or examined holistically, with all biological components and their interactions defined. Questions remain about how man-made reef habitats have compensated for functional losses in natural reef habitats or other sheltering habitats, such as eel grass beds, caused by man-made alterations, such as excessive nutrient and silt inputs, and toxic pollution.

Not all reef-associated organisms are benign or beneficial. Some "reef" species can be nuisances or cause human-interaction problems, e.g. wood-destroying Teredo "shipworms," gribbles, and other borers that attack wooden pilings and vessels; fouling organisms that inhibit vessel use efficiency, weigh down navigational aids, and fill pipelines that cycle estuarine or marine waters. Other species can be a source of larval resource species predators, e.g. carnivorous coelenterates such as anemones, or support the sessile stages of "jellyfish," such as *Chrysaora quinquecirrha* and *Cyanea capillata*.

Besides these nuisance organisms, the obvious hazards to vessel navigation and safety, and causing the loss of towed fishing gear and anchors, reefs have other negative side effects.

Wooden shipwrecks and other submerged wooden structures can be reservoirs and sources of the nuisance borers, noted above, which can attack wooden (and some concrete and plastic-coated) pilings within harbors (Nigrelli and Riccuiti, 1970). All man-made artificial reefs are subject to degradation processes to variable degrees (depending on the material used and the severity on environmental conditions they are exposed to) and some types were formerly subject to movement of certain reef material out of permitted reef sites, such as automobile tires, which interfered with other uses of the coastal zone, e.g. trawling and bathing. This problem mostly occurred in the early formative and experimental phases of artificial reef development, although some old artificial reefs are still the source of material lost from the reef sites.

Another aspect of the creation of reef habitat (accidental or intentional) on open bottom is that the reef and its associated community displaces previous open bottom communities (Shipp, 1999). It is normally assumed that open bottom habitat is not limited, at least in the Bight, and that open habitat loss caused by the development of new reef habitats will not significantly effect the function of this habitat to support desired population levels of other managed demersal species. It is also a value judgement of whether the reef habitat fishery resource community is of equal or greater value as a harvestable or economic resource, than to that of the soft-bottom community it replaces. These issues are not easy to resolve, and little information is available for such comparisons.

Several reef-associated fishery species are presently considered over- or fully exploited; these include Atlantic cod, haddock, pollack, scup, black sea bass, ocean pout, tilefish, striped bass, and American lobster (Clark, 1998; NMFS, 1999b). Oysters (as a fishery resource in this region) persist in declining natural beds and under culture; but the profitability of labor-intensive culture is declining because of increasing costs and stagnant prices per bushel, and continued investment in maintaining these beds is in ques-

tion (C. MacKenzie, Jr.[2]). Although the role of habitat in the conservation of these species is still poorly understood, reef habitat losses, at least in estuarine nursery grounds, can be suspected as being contributory (Rothschild et al., 1994).

Human Threats to Bight Reef Habitats and LMR's

Threats to reef habitats, in general, have been discussed by Bohnsack (1992), with emphasis on coral reefs. He noted inadequate knowledge of reef functions, a variety of habitat effects discussed below, and overfishing as being responsible for causing alterations in reef community structure and fishery productivity. There are the "normal" or natural threats to reef communities, as well, including damage from severe storms or other climatic events, and geophysical processes, such as changes in sea level and temperatures, but the scope of these natural threats is usually beyond human management.

A listing of most other threats to temperate reef habitat in the Bight, besides those named by Wilbur and Pentony (1999), includes, in no particular order:

1) Removal of reef habitats deemed navigational hazards or for channel deepening.
2) Siltation of reef habitats owing to ineffective land or coastal soil erosion control, or increased resuspension and distribution by vessel traffic, dredging, etc., which also causes the loss of low-structure, submerged aquatic vegetation (SAV) beds.
3) Damage to older wrecks and to algae and coral beds by towed fishing gear and large anchors (and in the 19th century by dynamiting wrecks to get valuable metals and to harvest fish).
4) Burial by dredged material disposal, including beach sand nourishment loss of shallowwater wrecks, and by shoreline jetties and groins.

5) Discharges or accidental coastal spills of toxic materials.
6) Removal of docks and piling fields in urbanized estuaries; these fields may replace lost shoreline trees, and SAV or oyster beds and other submerged or partially submerged natural habitat formerly available as LMR habitat.
7) Nonpoint source pollution in estuarine and coastal waters, some of which can be toxic to reef dwellers.
8) Loss of biogenic reef habitat, such as oyster and mussel beds, because of disease, overharvesting, other factors in this listing or unknown factors (Rothschild et al., 1994).
9) A strong preference or dependence on reef habitats can cause reef fish and lobster mortalities during occasional estuarine-coastal episodes of anoxia/hypoxia (Ogren and Chess, 1969; Steimle and Sindermann, 1978).
10) Power plant water use can kill the eggs and larvae of reef-associated species that are generally available in waters drawn into the plants, but especially from the spawning of species that use the rip rap or other hard surface linings of water intake canals or conduits as reef habitat.
11) Coastal or estuarine sand mining and redistribution activities.

Man-made Reefs as LMR and Habitat Management Tools

The planned placement of reef structures is a habitat management action, and this management action can be applied for various purposes, besides that of traditional fishery enhancement or one-to-one reef habitat replacement. Below is a list of habitat or fishery issues that can be addressed by reef habitat conservation, expansion, or manipulation, in no particular order:

1) Habitat fragmentation: Artificial reefs can mediate loss of structured habitat (reefs and SAV), especially in estuaries (Rothschild et al., 1994; Eggleston et al., 1998). The continued input of man-made reef material (intentionally or otherwise) into the environment is reducing natural

habitat fragmentation for reef-associated species and perhaps supporting their population expansions, especially on the continental shelf south of Long Island where reef habitat is naturally limited (Fig. 2). The system of wrecks and man-made reef-like structures across and along the continental shelf and coastal areas has created an array of reef habitats (only partially evident on Figure 6 owing to the limitations of the NOS database) that can act as corridors or a network that better supports the migrations or other movements of shelter-using species, such as black sea bass and American lobster, than occurred a century or two ago. Although, in the absence of better shelter, fish and megafauna often create or use previously created shallow depressions in soft sediments or low-profile biogenic structure (e.g. amphipod, polychaete, or anemone tubes) or molluscan shell accumulations for shelter (Auster et al., 1995).
2) Maintain biodiversity: Hard-bottom or reef habitats maintained or introduced among other habitat types, such as flat sand or mud bottoms, can increase habitat structural and biodiversity for algae, invertebrates, and fish (Sebens, 1991).
3) Provide refuge from excessive or damaging fishing: Introduction of solid high profile and complex-surfaced reef structures into an area can restrict the use of certain towed fishing gear in that area and promote a refuge function (Bombace, 1997). Artificial reefs that are under the control of state or Federal fishery resource agencies can be established as special management zones, reserves, or refuges from all or most harvesting (Bohnsack, 1992).
4) Expand limiting habitat: In some areas of the Bight, reef-associated fauna can be habitat limited because of inter- and intra-species competition for shelter (Richards and Cobb, 1986). As the density of all types of reef structures increase in the Bight and are more widely distributed across the open, sandy bottom, there will be more opportunity for

epifaunal species with relatively short lived larvae to find suitable habitat for colonization and thus gradually expand the distribution of hard surface, reef dwellers.

5) Maintain access for land-based fisheries: Some reef-like structures in estuaries, such as obsolete docks and piers in ports, can be preserved or maintained because, besides attracting certain fishery resources or their prey to submerged structures, they can also be used by human urban dwellers to support subsistence or low-income recreational fisheries (Hawkins et al., 1992; Able et al., 1998). Docks and piers also offer physically disabled people more opportunities to participate safely and comfortably in recreational fishing.

6) Estuarine/coastal nutrient removal: Experiments with artificial reefs suggest an abundant filter-feeding epifauna supported by reef surfaces, such as mussel populations, can potentially reduce and entrain eutrophic phytoplankton production in a reef area and in some cases reduce nutrients when attached algal colonies are established (Laihonen et al., 1997).

7) Compensation for unavoidable habitat loss: In cases where aquatic habitat loss is unavoidable, and in-kind habitat replacement is not available or feasible, reef habitats can be used to enhance productivity of fishery forage species, if not fishery species, as out-of-kind mitigation (Burton et al., 1999).

8) Provide opportunities for scientific research: The ability to plan the deployment and design of artificial reefs offers a range of opportunities for scientists to test hypotheses about issues, including the behavior of reef-associated species, the role of habitat size and complexity in species' use, and a number of other topics, such as those discussed below.

**Information Deficiencies
and Research Needs**

Because of the difficulty in surveying many reef habitats without the use of divers or remote in situ cameras, much

less is known about these habitats and their associated biological and fishery communities than is known for open seabed habitats and communities, and often only anecdotal information or observations are available. However, shipwrecks and reefs are now being given serious scientific attention as habitat for epifauna and fishery resources (Leewis and Waardenburg, 1991). But the characteristics and advantages of this habitat and its biological association are not considered in analyses and multiple regression models of associations among mixed demersal species, which often use only bathymetric and thermal metrics, but not benthic habitat structure as a distribution variable (Colvocoresses and Musick, 1984; Murawski and Finn, 1988). The developers and managers of artificial reefs for recreational fishing have noted some of their general information needs (Steimle and Meier, 1997), and these include: feasibility of estuarine applications, a better understanding of noncoral reef community ecology, better information on the life histories of reef-associated species, best reef designs for different applications and situations, better information on the population dynamics of reef resources, more information on reef productivity compared to other habitats, more information on the use of reefs to mitigate habitat loss, and socioeconomic data on the value of reef fisheries.

Some other specific information needs for the Bight include, in no particular order:

1) Diurnal and seasonal use of Bight reef habitats by LMR species.
2) Use of Bight reef habitats by the early benthic phase of LMR species.
3) Winter habitat requirements of south and offshore migrating Bight LMR's with strong summer reef-associations, e.g. black sea bass and scup.
4) Role of man-made reef habitat in conserving and enhancing fishing resources is poorly known, including the use of these reefs as refuges or reserves.
5) Ecology and LMR species use of deep-water reefs, besides the submersible studies associated with tilefish and submarine canyon habitat.

6) Ecological stability and dynamics of epifaunal communities should be better studied because many "fouling" species are relatively unstable and unpredictable in time and space because of their unpredictable recruitment and low survivorship, although some encrusting communities of bryozoans, compound ascideans, colonial cnidaria, and sponges are long-lived. (Dayton, 1984), and little is known of long-term community dynamics of subtidal reef communities, which can have several community states, some to the disadvantage of fishery resources, i.e. when coelenterates dominate (Steimle et al., 1999a).
7) To support the development of EFH parameters for managed fishery resources associated with structures or reefs, an inventory of significant structured habitats and concentrations of habitats with limited structural components, e.g. shell fields that may be important to juveniles, are needed, especially in the Bight. More side-scan sonar surveys are needed to define the distribution and abundance of hard-bottom and reefs in estuarine and marine waters, as per Smith and Greenhawk (1998), and to define, document, and monitor the shape and surface complexity of various wrecks and reefs and link this with LMR use.
8) Small scale spatial studies of the functional aspects (use) of reef habitats are needed especially to relate the size and complexity of reef habitats and interactions with hydrographic environment with LMR use (Auster, 1988).
9) The experimental approaches that are conducted in warmer temperate or tropical waters on the use and value of reef habitat, and the interrelationships of habitat size, shape, and complexity of fishery species use (Bohnsack et al., 1994) need to be attempted in the cooler temperate waters of the Bight to address similar information issues.
10) The generators of waste materials that are not readily or cost-effectively recyclable or disposed of on

land, will continue to consider the sea as an disposal option and a wide diversity of solid materials, including nonsolids such as incineration ash incorporated into a solid matrix such as concrete, are often proposed for use in developing artificial reef materials. Inadequate information is usually available on the sustained value of these diverse materials as non-toxic and positive habitats for fishery resources.

11) Models are needed to explore the effects of changing the density or distribution of artificial reef habitats on resident or seasonal fishery resource population dynamics and movements.

Summary

Man-made habitats have become a growing integral part of the coastal and shelf ecosystem in the Bight over the last 150 years and they support populations of managed fishery resources, at least seasonally. Recognition of these habitats, their availability, and their use by fishery resources can support the use of this information in fishery resource population abundance estimates (these habitats can be a refuge from survey trawls).

Recognition of this habitat can help understand the probable migration pathways of shelter-associated species that may benefit from the growing array of man-made reef habitats. Recognition is a step toward conserving and making better use of this habitat to support appropriate fishery management goals, by habitat manipulation or enhancement, and thus diversifying fisheries in many areas. This summary is also a preliminary effort towards developing a baseline habitat inventory for the Northeast Region.

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A Preliminary Study of the Marine Biota at Navassa Island, Caribbean Sea

MARK GRACE, MELISSA BAHNICK and LISA JONES

Introduction

During the 1998 U.S., Mexico, and Cuba shark assessment cruise (Grace[1]), Navassa Island was included as a study site. Primary objectives there were to determine what reef fish and shark populations were present and to collect associated environmental data at

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ABSTRACT—A preliminary study of reef fish and sharks was conducted at Navassa Island in the Caribbean Sea during a 24-h period beginning 9 September 1998. Conducting a study at Navassa Island was of particular interest because exploitation of Navassa Island's fishery resources has been considered minimal due to its remote location (southwest of the Windward Passage, Caribbean Sea) and lack of human habitation. Reef fish (and associated habitats) were assessed with stationary underwater video cameras at 3 survey sites; sharks were assessed by bottom longlining at 5 survey sites. Fifty-seven reef fish identifications to lowest possible taxon were made from video footage. Longline catches produced 3 shark species and 3 incidental catch species. When results from the 1998 National Marine Fisheries Service (NMFS) project are combined with a previous 1977 NMFS survey of Navassa Island, 27 fish families, 79 fish identifications to lowest possible taxon, 4 invertebrate orders or families, 3 coraline families, and 2 macroalgae phyla are reported.

survey sites. Survey activities included use of underwater video cameras to record reef fish assemblages and sea bottom characteristics at selected video sites; bottom longlining was also conducted to assess shark relative abundance (Table 1).

The opportunity to assess fish populations at Navassa Island was important for several reasons, including its status as one of the last unexploited islands in the Greater Antilles. Many Caribbean nations have experienced over-exploitation of fishery resources during recent decades, and conditions for improvement of fishery stocks do not seem likely considering demand for fish products as a protein source (Munro, 1996). Oceanic conditions are another factor that can influence the status of Caribbean reef fish populations since overexploitation potentially affects fish populations downstream of recruitment sources (Roberts, 1998). Therefore, the importance of Navassa Island as a likely source of recruits to neighboring Caribbean areas and as an important habitat for viable fish stocks should be established.

Navassa Island, an uninhabited U.S. possession in the Caribbean Sea located between Haiti and Jamaica (Fig. 1), was claimed by the United States as a part of the 1857 Guano Act. In 1997 the U.S. Coast Guard transferred stewardship of the island to the U.S. Department of Interior which issued a general research permit to NMFS to conduct the 1998 survey.

Navassa Island is a flat-topped prominence (maximum elevation 77 m) of about 5.2 km^2 in size. A shallow reef is present at the northwestern tip of the island, but most bottom depths adjacent to shore begin at 20 m with a gradual

depth increase to 40 m (Fig. 1); bottom depth increases are more pronounced beyond 40 m, with depths up to 500 m within 0.8 n.mi. of the north shore. The bottom type is coarse sand with broad areas of live bottom (corals, sponges, and algae), limestone rock, and rubble. The shore of Navassa Island is principally limestone cliffs with a small area along the north coast consisting of a steep rocky beach with some sand. The island is covered with dense tropical foliage, primarily palm trees with brush undergrowth and cactus. An abandoned lighthouse and relic building ruins are located midway along the western shore (Fig. 2). Numerous seamounts within its territory (Exclusive Economic Zone) are unique features for the northeast region of the Caribbean Sea.

Materials and Methods

To collect underwater video footage, four Hi-8 video cameras[2] with wide-angle (120°) lenses were fixed in underwater camera housings (rated to 109 m depth). Cameras were attached orthogonally to a metal camera-support frame (weighted), and deployed with buoys. The 4-camera array was baited with 0.5 kg Atlantic mackerel, *Scomber scomber*, suspended in a mesh basket at the center of the array.

Prior to deployment of video 4-camera arrays, the survey sites' bottom type was assessed with the ship's echosounder to determine presence of bottom features (reef structure) or above-bottom return signals (fish). Due to ship safety concerns, survey operations were not conducted within 0.3 n.mi. of shore. Camera

Figure 1.— Survey sites at Navassa Island, *Oregon* II survey 98-02 (231).

Table 1.—Survey site locations and associated environmental data (maximum gear depth) from Navassa Island (1998).

Location (lat./long.)	Gear	Depth (m)	Time (h)	Temperature (°C)	Salinity (ppt)	Dissolved oxygen (mg/l)	Turbidity (% transmittance)	Chlorophyll (mg/m³)	Effort
18°25.85'N/75°01.84'W	Longline	342.0	0627	16.48	36.26	4.9	0.02	0.0732	2 h
18°24.90'N/75°01.99'W	Video #1	29.9	1000	29.40	36.10	4.7	0.10	0.0178	5 h 50 min
18°23.32'N/75°01.02'W	Video #2	28.0	1409	29.55	36.09	4.8	0.02	0.1368	4 h 26 min
18°24.37'N/74°59.85'W	Video #3	38.3	1757	29.45	36.07	4.8	0.02	0.176	3 h 28 min
18°23.52'N/74°59.37'W	Longline	272.1	2043	16.20	36.22	4.8	0.05	0.081	2 h
18°24.84'N/74°59.63'W	Longline	240.0	0107	16.70	36.27	4.9	0.02	0.076	2 h
18°23.67'N/75°01.89'W	Longline	224.0	0548	18.76	36.60	4.6	0.05	0.085	2 h
18°22.82'N/75°00.75'W	Longline	272.0	0956	18.82	36.62	5.0	0.05	0.081	2 h

drops were made in areas that were determined to be reef habitats; camera drops were not conducted in areas that appeared to be nonreef or devoid of above-bottom return signals. Camera drops were located in approximate triangulation around Navassa Island to provide a measure of coverage.

Five bottom longline survey sites were selected around the island's perimeter and parallel to depth contours when possible. Since the length of the longline (1 n.mi.) was almost equal to the length of Navassa Island, longline sets were relatively close together. The start point for longline sets was estab-

lished by dividing the perimeter of Navassa Island into 5 relatively uniform (by size) sampling zones then selecting a random point within each zone. Direction of longline sets was often dependent on sea and weather conditions and sets were configured so they would not overlap with adjacent longline sites.

Figure 2.—Navassa Island lighthouse and western shore.

The survey platform NOAA Ship *Oregon* II (Fig. 3), was outfitted with commercial-type longline gear for conducting longline operations. Monofilament mainline (426 kg test, 1 n.mi. length) was directed to the stern with longline components attached to the mainline during longline sets (3.7 m gangions of 332 kg monofilament with #3/0 shark hooks, radar reflector buoys, 5 kg weights). Hooks (50) were baited with Atlantic mackerel that was either whole or cut in half, and gear soak time was about 2 h for each set.

Environmental data were collected with a CTD deployed at each survey site. The CTD provides a surface to bottom profile of temperature, salinity, dissolved oxygen, turbidity, and chlorophyll.

Results

Reef fish were identified from video footage (13 h 44 min total) collected at 3 video sites (Fig. 1 and Table 1). Video

footage recorded with each camera of the 4-camera array was reviewed. Species identifications from video footage were made by family, genus or species (lowest possible taxon; some fish identifications were possible only to family or genus due to far-field resolution). Fifty-seven reef fish identifications to lowest possible taxon representing 20 families were made from video footage collected at the 3 video sites (Table 2). It was not uncommon to record several reef fish species in the same video frame. If reef fish were numerous, video segments had to be reviewed a number of times to determine species identifications.

While recording video footage at video sites #2 and #3, the camera-support frame repositioned to its side (due to currents or bottom irregularities) and the camera view changed which affected video documentation of reef fish at those sites. Every effort was made to utilize as much footage as possible for

identifying reef fish. In addition, video footage collected at video site #3 was affected by end-of-the-day decreasing ambient light. Enumerating reef fish from video footage was not attempted since only video site #1 provided footage adequate for enumerations; however, members of reef fish families Pomacentridae, Labridae, and Scaridae were abundant at all 3 video sites.

From video footage reviews it was possible to discern bottom characteristics and associated encrusting organisms at video sites (Table 3). At the northwest video site (#1) the bottom was of relatively even relief with thick patches of soft corals, sponges, and algae; the southernmost video site (#2) had irregular low clumps of rock and encrusting organisms surrounded by sand and thick patches of sea feathers (*Pseudopterogorgia*); the northeastern video site (#3) had numerous clumps or mounds (estimated at 1 m height, 2–4 m diameter, possibly limestone)
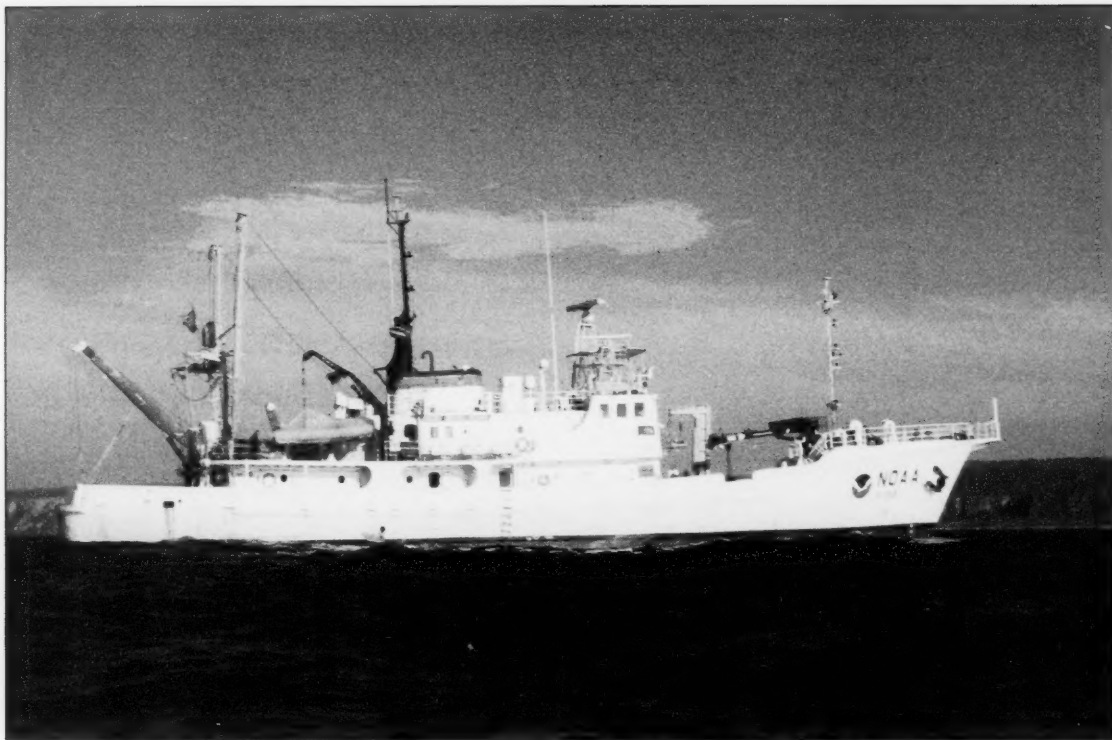
Figure 3.—NOAA Ship *Oregon* II.

capped with soft corals, sponges, and algae. Porifera (sponges), Octocorallia (soft corals), and Chlorophyta (green alga) were found in common at the 3 video sites.

Bottom longline effort produced 10 shark captures (Table 4), and the predominant shark captured was the scalloped hammerhead, *Sphyrna lewini*. The highest shark catch rate occurred at the west-southwest longline site with 6 captures (5 scalloped hammerheads and 1 smooth dogfish, *Mustelus canis*). Incidental captures from longline sites included 1 misty grouper, *Epinephelus mystacinus*; 1 silk snapper, *Lutjanus vivanus*; and 1 great barracuda, *Sphyraena barracuda*.

Bird observations were opportunistic (made both unaided and with binoculars), with identifications to genus and species. Species included Cory's shearwater, *Calonectris diomedo*; magnificent frigatebird, *Fregata magnificens*; cliff swallow, *Hirundo pyrrhonota*; Bonaparte's gull, *Larus philadelphia*; Pomarine jaeger, *Stercorarius*

pomarinus; masked booby, *Sula dactylatra*; brown booby, *Sula leucogaster*; and red-footed booby, *Sula sula*. Extensive booby nesting areas (identification to species not possible) were noted in treetops along the south side of the island with at least 40 nests observed with young birds roosting.

Discussion

Since 1900 there have been few scientific expeditions to Navassa Island (conducted principally to assess terrestrial fauna: Ekman, 1929; Clench, 1930; Burns et al., 1959), and there are no published records from those expeditions describing marine fauna beyond the splash zone. Recent marine fauna studies of Navassa Island include a project conducted by NMFS in 1977 (Miller[3]) and 1998, 1999, and 2000 projects (detailed survey results

[3] Miller, G. 1977. Cruise results for *Oregon* II 77-08 (80), Navassa Island resource assessment survey. Cruise report, 12 p., on file at NMFS Southeast Fisheries Science Center Miami Laboratory, 75 Virginia Beach Dr., Miami, FL 33149.

are not yet available) sponsored by the Center for Marine Conservation (CMC) (Smith[4]). The 1977 NMFS survey deployed hook and line gear, wire and wood crustacean traps, a tumbler dredge, trolling rigs, neuston and icthyoplankton nets, dipnets, and snorkel diver operations. When results from the 1977 and 1998 NMFS projects are combined, 27 fish families, 79 fish identifications to lowest possible taxon, 4 invertebrate orders or families, 3 coraline families, and 2 macroalgae phyla are reported (Tables 2, 3). Macroalgae was recorded on video footage from all 1998 NMFS camera drop sites (Table 3), and the 1977 NMFS Navassa Island report (Miller[3]) also confirmed the presence of macroalgal reefs.

The concept of Navassa Island as a pristine and entirely unexploited marine habitat must be viewed with caution. Miller[3] mentions Haitian fishermen in-

[4] Smith, M. 1998. Center for Marine Conservation, 1725 DeSales St. N.W., Wash., DC 20036. Personal commun.

Table 2.—Fish identified at Navassa Island during 1998 and 1977. Gear types: trolling = Tr, trap = T, pole and line = P, dredge = D, snorkel diver = Sn, longline = L, video camera = V.

Family and scientific names	Common name	1998	1977	Family and scientific names	Common name	1998	1977
Carcharhinidae				Chaetodontidae (continued)			
Carcharhinus leucas	Bull shark	L		Chaetodon sedentarius	Reef butterflyfish	V	
Triakidae				Pomacanthidae			
Mustelus canis	Smooth dogfish	L		Holacanthus tricolor	Rock beauty	V	
Sphyrnidae				Pomacanthus arcuatus	Gray angelfish	V	
Sphyrna lewini	Scalloped hammerhead	L		Pomacentridae			
Urolophidae				Pomacentridae	Damselfishes	V	
Urolophus jamaicensis	Yellow stingray	V		Chromis sp.	Damselfish	V	
Muraenidae				Chromis cyanea	Blue chromis	V	
Gymnothorax moringa	Spotted moray		T	Chromis multilineata	Brown chromis	V	
Antennariidae				Microspathodon chrysurus	Yellowtail damselfish	V	
Antennarius multiocellatus	Longlure frogfish		D	Pomacentrus sp.	Damselfish	V	
Holocentridae				Pomacentrus partitus	Bicolor damselfish	V	
Holocentrus sp.	Squirrelfish	V		Pomacentrus planifrons	Threespot damselfish	T	
Holocentrus adscensionis	Squirrelfish	V	T	Sphyraenidae			
Holocentrus marianus	Longjaw squirrelfish		T	Sphyraena barracuda	Great barracuda	V, L	Tr, Sn
Holocentrus rufus	Longspine squirrelfish		T	Labridae			
Aulostomidae				Labridae	Wrasses	V	
Aulostomus maculatus	Trumpetfish	V		Bodianus rufus	Spanish hogfish	V	
Serranidae				Clepticus parrae	Creole wrasse	V	
Hypoplectrus sp.	Hamlets	V		Halichoeres garnoti	Yellowhead wrasse	V	
Hypoplectrus puella	Barred hamlet	V		Thalassoma bifasciatum	Bluehead wrasse	V	
Serranus tigrinus	Harlequin bass	V		Scaridae			
Cephalopholis cruentatus	Graysby	V		Scaridae	Parrotfishes	V	
Cephalopholis fulvus	Coney	V	P	Scarus sp.	Parrotfish	V	
Epinephelus guttatus	Red hind	V	P	Scarus taeiopterus	Princess parrotfish	V	
Epinephelus mystacinus	Misty grouper	L		Sparisoma atomarium	Greenblotch parrotfish	V	
Mycteroperca rubra	Comb grouper		D	Sparisoma aurofrenatum	Redband parrotfish	V	T
Mycteroperca tigris	Tiger grouper		Sn	Sparisoma viride	Spotlight parrotfish	V	
Paranthias furcifer	Creolefish	V	P	Gobiidae			
Rypticus saponaceus	Greater soapfish	V		Coryphopterus personatus/hyalinus	Masked/Glass goby	V	
Malacanthidae				Acanthuridae			
Malacanthus plumieri	Sand tilefish	V	P	Acanthurus sp.	Tangs	V	
Carangidae				Acanthurus bahianus	Ocean surgeon	V	T
Elagatis bipinnulata	Rainbow runner		P	Acanthurus coeruleus	Blue tang	V	
Seriola sp.	Jacks		Sn	Scombridae			
Caranx sp.	Jacks	V		Thunnus atlanticus	Blackfin tuna	Tr	
Carnax bartholomaei	Yellow jack	V		Balistidae			
Caranx latus	Horse-eye jack		P	Balistidae	Triggerfish	V	
Caranx lugubris	Black jack		P	Balistes vetula	Queen triggerfish	V	P, T
Caranx ruber	Bar jack	V	P	Canthidermis sufflamen	Ocean triggerfish	V	P, Sn
Lutjanidae				Melichthys niger	Black durgon	V	P, Sn
Lutjanus sp.	Snappers	V		Xanthichthys ringens	Sargassum triggerfish	V	
Lutjanus apodus	Schoolmaster snapper		Sn	Cantherhines macrocerus	Whitespotted filefish	V	
Lutjanus jocu	Dog snapper	V	Sn	Ostraciidae			
Lutjanus vivanus	Silk snapper	L		Lactophrys sp.	Boxfish	V	
Ocyurus chrysurus	Yellowtail snapper	V	Sn	Lactophrys bicaudalis	Spotted trunkfish		T
Haemulidae				Lactophrys polygonia	Honeycomb cowfish	V	
Haemulon album	White margate		P	Lactophrys trigonus	Trunkfish	V	
Mullidae				Tetraodontidae			
Pseudupeneus maculatus	Spotted goatfish	V	T	Canthigaster rostrata	Sharpnose puffer	V	
Kyphosidae				Diodon sp.	Burrfishes		Sn
Kyphosus sp.	Chubs	V	Sn				
Chaetodontidae							
Chaetodon aculeatus	Longsnout butterflyfish	V	D	Totals (to lowest taxon)		63	33

habiting the island, and during the 1998 NMFS project fishing activities from a small sailboat (about 3–4 m length) were observed. This boat sailed to Navassa Island from the east and fishermen checked fishing gear along the south side of the island.

Conclusion

The value of Navassa Island as a unique marine habitat can be established through continued studies of its marine ecosystem. Since Navassa Island is uninhabited and remote, it could provide an important platform for researchers to examine a Greater Antilles habitat that may remain in a relatively unexploited state.

During April 1999, Navassa Island was declared a National Wildlife Refuge. This refuge designation encompasses the island and surrounding 12-mile territorial sea. The U.S. Department of the Interior's, U.S. Fish and Wildlife Service administers Navassa Island through their Caribbean Islands Refuges Office in Boqueron, Puerto Rico.

Acknowledgments

Table 3.—Benthic invertebrates and marine plants of Navassa Island (1998 and 1977). Gear types: D = tumbler dredge, Sn = snorkel diver, V = video.

Family and scientific names	Common name	Gear types 1998	Gear types 1977	Family and scientific names	Common name	Gear types 1998	Gear types 1977
Porifera				Mollusca (continued)			
Agelas schmidti	Pipes of Pan sponge	V		*Lima lima*	Spiny fileclam		D
Xestospongia muta	Basket or tub sponge	V		*Lima scabra*	Rough fileclam		D
Demospongia	Unidentified	V	D	*Malleus candeanus*	Caribbean hammer oyster		D
Hydrozoa				*Murex cabritii*	Murex		D
Fire coral unidentified			D	*Perotrochus pyramus*	Slitsnail		D
Octocorallia				*Purpura patula*	Widemouth rocksnail		D
Plexaura sp.	Sea rods	V		*Spondylus ictericus*	Digitate thorny oyster		D
Pseudoplexaura sp.	Porous sea rods	V		*Strombus gallus*	Roostertail conch		D
Pseudopterogorgia sp.	Sea plumes	V		*Trachycardium magnum*	Magnum pricklycockle		D
Gorgonacea	Unidentified soft corals	V		*Turritella exoleta*	Eastern turretsnail		D
Hexacorallia				*Verticordia fischeriana*	Fischer verticord		D
Acropora palmata	Elkhorn coral		Sn	Crustacea			
Diploria sp.	Brain coral		Sn	Anomurans	Hermit crabs		D
Scleractinia	Stony coral		S	Echinodermata			
Mollusca				Asteroidea	Sea stars		D
Americardia media	Atlantic strawberry cockle		D	Crinoidea	Crinoids		D
Argopecten gibbus	Atlantic calico scallop		D	Chlorophyta			
Bathytoma viabrunnea	Turrid shell		D	*Halimeda* sp.	Green algae	V	
Calliostoma aurora	Topsnail		D	*Penicillus* sp.	Shaving brushes	V	
Cittarium pica	West Indian top snail		D	Phaeophyta			
Conus villepini fosteri	Cone shell		D	*Dictyota* sp.	Strap algae	V	
Coralliophila caribaea	Caribbean coralsnail		D	*Lobophora* sp.	Fan leaf algae	V	
Cypraea cinerea	Atlantic gray cowrie		D	Unspecified Algae			D
Laevicardium sybariticum	Delicate eggcockle		D				
Leucozonia nassa	Chestnut latirus		D	Totals to lowest taxon		11	29

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Table 4.—Summary of bottom longline captures from 1998 NMFS Navassa Island project (50 hooks set for 2 h at each of 5 bottom longline stations).

Scientific name	Common name	No. captured	Total length (cm)
Carcharhinus leucas	Bull shark	1	170
Mustelus canis	Smooth dogfish	2	96, 101
Sphyrna lewini	Scalloped hammerhead	7	224, 225, 230, 250, 250, 275, 300
Epinephelus mystacinus	Misty grouper	1	78
Lutjanus vivanus	Silk snapper	1	72
Sphyraena barracuda	Great barracuda	1	185

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Reported Trip Costs, Gross Revenues, and Net Returns for U.S. Atlantic Pelagic Longline Vessels

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Introduction

The U.S. Atlantic pelagic (midwater) longline fleet harvests a multitude of species. In a recent study by Cramer and Scott[1], over 30 species were included in a catch-effort analysis of the fleet. In 1996, approximately 75% of the trips reported landing swordfish, *Xiphias gladius*, 65% reported landing at

[1] Cramer, J., and G. P. Scott. 1998. Summarization of catch and effort in the pelagic longline fishery and analysis of the effect of two degree square closures on swordfish and discards landings. U.S. Dep. Commer., NOAA, NMFS, Sustainable Fisheries Division Contribution MIA-97/98-17, 22 p. Avail. from NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149.

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ABSTRACT—Logbook set and trip summary data (containing catch and cost information, respectively) collected by NOAA's National Marine Fisheries Service (NMFS) were analyzed for U.S. pelagic longline vessels that participated in Atlantic fisheries in 1996. These data were augmented with vessel information from the U.S. Coast Guard. Mean fish weights and ex-vessel prices from NMFS observers and licensed seafood dealers, respectively, were used to estimate gross revenues. Comparisons revealed that net returns varied substantially by vessel size and fishing behavior (i.e. sets per trip, fishing location, season, and swordfish targeting). While the calculated economic effects of proposed regulations will depend on the descriptive statistic chosen for analysis, which itself depends on the type of analysis being conducted, results show that considering heterogeneity within this fleet can have a significant effect on predicted economic consequences.

least one of the BAYS tunas (i.e. bigeye, *Thunnus obesus*; albacore, *T. alalunga*; yellowfin, *T. albacares*; and skipjack, *Katsuwonus pelamis*), and 55% reported landing dolphin, *Coryphaena hippurus*. In addition, nearly one-third landed coastal sharks, including sandbar, *Carcharhinus plumbeus*; silky, *C. falciformis*; blacktip, *C. limbatus*; dusky, *C. obscurus*; and hammerheads, *Sphyrna lewini, S. mokarran, and S. zygaena* (Larkin et al.[2]). Landings of pelagic sharks and other species such as wahoo, *Acanthacybium solanderi*; oilfish, *Ruvettus pretiosus*; and blackfin tuna, *Thunnus atlanticus*, were also reported in relatively large numbers.

Increasingly stringent domestic regulations on individual stocks, including the highly migratory species (HMS), have affected vessels that target multiple species (NMFS, 1999a). The additional regulatory pressure, in part, has caused some Atlantic pelagic longline (PLL) vessels to adopt gear that 1) simultaneously targets multiple species or 2) can easily be modified to target other species once shark and swordfish quotas are met (South Atlantic Fishery Management Council[3]). The increasing trend toward multi-species targeting by PLL vessels indicates that traditional single-fishery economic analyses may overlook benefits and costs that are unique to multi-species opera-

[2] Larkin, S. L., D. J. Lee, and C. M. Adams. 1998. Costs, earnings, and returns to the U.S. Atlantic pelagic longline fleet in 1996. Food and Resource Economics Staff Paper SP 98-9, 44 p., avail. from University of Florida, P.O. Box 110240, Gainesville, FL 32611-0240.

[3] South Atlantic Fishery Management Council. 1997. Options paper for management of dolphin fish, 12 p., avail. from SAFMC, One Southpark Circle, Suite 206, Charleston, SC 29407.

tions. If so, reliance on economic analyses that only incorporates a single species may result in a suboptimal resource management decision (Wilson, 1982).

Atlantic sharks and North Atlantic swordfish are managed in the United States under authority of the Magnuson-Stevens Fishery Conservation and Management Act (the Magnuson-Stevens Act). Tunas and billfish, including swordfish, are also managed under the authority of the Atlantic Tunas Convention Act. A recently released fishery management plan (FMP) for HMS integrates the domestic management of Atlantic tunas, swordfish, and sharks pursuant to the Sustainable Fisheries Act (NMFS, 1999a). This FMP acknowledges the multi-species nature of the commercial fisheries by accepting, for example, swordfish landings and permit histories as sufficient justification for receiving (at least) "incidental" shark and Atlantic tuna longline permits (NMFS, 1999b).

Prior to implementing or revising an FMP, the costs and benefits of the proposed regulations must be assessed. To this end, the Magnuson-Stevens Act requires a Regulatory Impact Review (RIR) to identify expected changes in the net economic benefits to society (e.g. gross industry revenues less harvest costs). In addition, the Regulatory Flexibility Act (RFA) requires an assessment of potential economic impacts on small entities, such as changes in gross revenues and/or fishing expenditures for individual operations or different industry segments (U.S. Small Business Administration, 1998). The overall importance of economic information was appropriately summarized in the recently authorized HMS FMP:

An integral part of an FMP or FMP amendment is an analysis of the economic effects of the various management alternatives. This economic analysis is critical to identify the preferred measures that minimize economic impacts while meeting overall management goals (NMFS, 1999a:7–2).

The formal collection of economic data from vessels participating in Atlantic pelagic fisheries was not implemented until 1996. At that time, questions regarding trip expenses and labor payments were added to the trip summary form. Although the economic portion of the form was voluntary, complete information was obtained on 642 trips taken by 125 PLL vessels operating in the Atlantic in 1996. These observations accounted for 20% of the total trips and included information from 47% of the fleet.

The purpose of this paper is to present descriptive statistics on the Atlantic PLL fleet using the first economic data collected. Means are used to describe data in which observations are distributed normally and medians are used for observations with skewed distributions; this is because when the distribution of a variable is skewed (such as is common with housing prices and income) it is customary to use the median value to measure the central tendency (Cavanos and Miller, 1993). Given the skewedness of the frequency distributions on the behavioral, cost, and landings variables for this fleet as shown in Larkin et al.[2], the use of fleet-wide means presented in that analysis would provide an inaccurate quantification of the "average" or "typical" trip and set for use in calculating changes in total gross revenues as used in an RIR. The potential insufficiency of aggregate mean (i.e. arithmetical average) statistics to describe central tendency was also identified in regards to completing the RFA analysis in the recent HMS FMP, which stated that "due to the multi-species and multi-natured operation of HMS fishing vessels (i.e. wide range in vessel size, mileage per trip, geographic differences in fuel costs, etc.), averages should be used cautiously" (NMFS, 1999a:7–31).

Perhaps more importantly, "[w]hile the RFA analysis and NMFS guidelines focus on gross revenues, net revenues are a more accurate measure of both income and the net economic effect of regulatory measures" (NMFS, 1998:18). Focusing on changes in gross revenues ignores cost differences that can offset projected revenue changes from a proposed policy. Given the skewed distributions and availability of cost data, the bulk of our analysis compares median statistics and, in particular, net revenues. Comparisons are also made using gross revenues, costs, and mean net revenues. By examining differences between aggregate statistics and statistics calculated using disaggregated data (by region, number of sets, swordfish revenues, etc.), the effects on the resulting economic analysis (e.g. RIR and/or RFA) can be quantified.

The Data and Methods section contains a description of the data and the procedures used to create a single comprehensive data set for the U.S. Atlantic PLL fleet. The discussion is detailed in order to provide transparency and full disclosure in the analysis as recommended by the Office of Management and Budget (1996). The level of detail also allows for replication of the data set and consistency with future data sets. This is important because using a different procedure, order of procedures, or changing the underlying assumptions would alter the data and thereby change the economic outcome predicted by policy analyses in a way that could yield significantly different results.

To interpret economic findings for the entire industry, the Results section begins with a comparison of the population means (i.e. data for all trips, sets, and vessels) with the means from a subset of the population to assess whether the economic information in the subset was representative of the whole. Median statistics are then calculated for gross revenues by species, the costs of fishing supplies, and the estimated returns per trip across different vessel and trip characteristics. The data are examined at the trip level (in part) because, according to Squires and Kirkley (1995: 156), "the vessel-trip level

represents the most complete disaggregate scale or level of production." In addition, the factors that affect trip expenses and landings (such as the quantity of fuel, bait, tackle, ice, and groceries and the type of bait and tackle) depend on the anticipated trip length, target species, season, and general area fished. The majority of these decisions (including the number of crew to hire) must be made prior to departure, remain constant during the trip, and affect decisions made during the trip. For these reasons, and since trip-level analysis was employed in the recent economic analysis of this fleet (NMFS, 1998; 1999a), trip-level aggregate and disaggregated analyses were included to provide additional useful information for this fishery.

In the Summary and Conclusions section, we briefly identify the main findings, reiterate the major assumptions, and consider how these data can be used in management decisions.

Data and Methods

This discussion focuses on the methods we used to 1) extract the PLL data from the pelagic fisheries data, 2) decide which vessel characteristics to consider (including how to define subgroups), 3) identify sources of fish weight and price data, and 4) define and calculate gross revenues, trip costs, and net returns.

NMFS requires U.S. vessels participating in Atlantic pelagic fisheries to submit 1) a record for each set including the gear used, fishing effort (length of mainline, number of hooks, type of bait, etc.), location, and numbers of each species kept (i.e. landings), and 2) a summary of each trip including the number of sets, departure and offloading ports and dates, and the first and last fishing days. These detailed summaries are often referred to as "set forms" and "trip forms," respectively, or generically as "logbook" forms or reports. In 1996, variable cost and payment questions were added to the trip summary form.[4]

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[4] All logbook data obtained from NMFS were in raw (as reported) form; however, the set data contained additional variables identifying observations with suspected problems. We note where this information was used in the text.

NMFS received 17,239 set forms in 1996. Our data validation began with identifying discrepancies between the number of sets reported on the trip form and the number of set forms submitted with the same trip number. It was important that these numbers match since the landings from the set forms are aggregated and used to estimate the gross revenue received from each trip. Most differences involved the case where only one set form was submitted for a trip that reported placing multiple sets on the trip form. For these observations, which were identified in the data set by NMFS, we assumed the number of sets reported on the trip form to be accurate and that the landings on the set form represented the entire trip (i.e. the set form was a "summary" set). We also compared the dates of first and last fishing days from the trip form to the date of the set. If the reported set date did not fall within the reported fishing dates, we compared the set date to the number and dates of the other sets and trips by the same vessel. In most cases, the correct set date was obvious. The discrepancies between the set and trip information highlight the importance of cross-validating responses.

Since the owners or captains of all commercial vessels that target pelagic species are required to submit set forms, the data set contained information on all gear types. Following Cramer and Scott[1], we used the number of hooks to identify PLL sets since there was a very high response rate associated with this variable. In particular, the set was considered to correspond with the use of PLL gear if at least 100 hooks were reported.[5] To avoid excluding PLL sets by vessels whose owner/captain failed to report the number of hooks used, we also retained set forms that indicated the use of either "pelagic longline" or "longline but not bottom longline" gear (i.e. one of those gear types was checked on the set form). To avoid excluding sets and trips by PLL vessels whose owner/captain failed to answer the question, we also retained the sets

and trips with corresponding trip and vessel numbers.[6] The remaining data set contained 16,549 sets placed during 3,352 trips by 276 vessels.

After aggregating the landings statistics from the set forms by trip number, we merged the resulting file with the corresponding trip logbook data. We deleted unmatched trip numbers from the file; these were observations with a trip summary form but without corresponding set forms and, thus, landings data.[7] The remaining data set contained 16,477 sets placed during 3,255 trips by 272 PLL vessels (i.e. 99.6% of total sets, 97.1% of total trips, and 98.6% of total vessels) operating in the Atlantic in 1996.

We supplemented the landings and cost data with vessel information maintained by the U.S. Coast Guard (USCG). The USCG requires all vessels displacing at least 4.55 net metric tons (t) (5 net tons) to register with the agency and receive a vessel identification number. We used the vessel identification number to obtain the displacement of each vessel. Nine vessels did not have a USCG number, which indicates they displace less than 5 net tons.

To determine gross revenues per trip, we turned to the 1996 trip logbook which included payments to the owner, captain, and the average paid to each crew member. Ideally, gross revenues would be determined by summing the owner, captain, and crew payments (i.e. the average payment times the number of crew) and knowing whether or when the various expenses were deducted. Given incomplete reporting (especially regarding the owner payment) and that information on how payments were determined was not collected, we could not estimate gross revenues from the reported payment information.

As an alternative to using the stated payments, we estimated gross revenues per trip from the landings data using mean weights and prices for each species. An advantage to using this approach is the ability to derive a gross revenue estimate for each species that reflects the underlying landings. In addition, the landings data may be more reliable since they are mandatory, submitted immediately upon docking, and less sensitive in nature than payment information.

For the fish weights, we first turned to the set logbook which asks for the total number of pounds kept. Ideally, these total weights would be used directly with price information to calculate gross revenue. In 1996, weight information was supplied for eight species and response rates ranged from 0.3% to 41%. Using the total weights with the landings for these species we computed mean individual weights for use with observations without data; however, the calculated mean weights were unrealistic, e.g. individual weights for yellowfin tuna ranged from 0.03–659 kg or 0.06–1,465 pounds. Given the extreme and unrealistic range of observed values (which could produce unrealistic gross revenue estimates) and the lack of information on the remaining species, we decided against using this information and instead opted for mean weights and prices from other NMFS data sources. The primary advantage of this approach is that NMFS has validated these data.

Licensed dealers are required to submit sales receipts, which are also known as "weight-out" sheets, containing the landed (i.e. dressed) weight of each fish purchased. Mean weights from these receipts in 1996 were the primary data source used in this study (Bertolino[8]). For species missing from the sales data, we used mean weights from the NMFS Southeast Region observer program (Lee[9]). Mean weights from either source were only used if

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[5] Unlike Cramer and Scott[1], sets reporting fishing locations that were missing or could not be verified were not removed.

[6] Since the indicated use of PLL gear is not mutually exclusive to the use of other gears on the set forms, our analysis can include catch from all gears used during a PLL trip; however, the incidence of that was relatively small. For example, of the total 16,477 PLL sets, 2 reported using harpoons, 161 reported using rod and reel gear, and 93 reported using handline gear.

[7] We considered deleting these trips (3% of the total) preferable to assuming zero landings, which would artificially lower the mean and possibly the median revenue statistics if the set forms were misplaced or not submitted.

[8] Bertolino, A. 2 March 1998. NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149. Personal commun.

[9] Lee, D. 16 January 1998. NMFS Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149. Personal commun.

calculated from at least three observations. We obtained mean weights for species not included in either the sales or observer data from the HMS FMP (NMFS, 1999a). The FMP was not the primary data source since the report utilized common weights for the following species groups: tunas, large coastal sharks, pelagic sharks, and other fish. The FMP also provided information on how to calculate the landed weight of shark fins (NMFS, 1999a).

We calculated mean prices for each species from total longline landings and dockside value as reported by dealers in the Atlantic and Gulf of Mexico region in 1996 (NMFS[10]). For species not included in the longline landings summary we used the mean price for all commercial landings by species. Using this method the mean price is the average price per pound round (i.e. live or undressed) weight. Since mean weights were only available on a dressed-weight basis, these prices would be underestimated by the dressed-to-round weight conversion factor. We obtained factors used to convert dressed weight (dw) landings to round weight (rw) for swordfish and the majority of tunas and sharks from NMFS (Bennett[11]). The Florida Department of Environmental Protection[12] provided the dw-rw conversion factors for the remaining species. Table 1 contains the total landings, conversion factors, and mean weights and prices for each species used to estimate total industry gross revenues for 1996.

Of the 3,255 PLL trips with reported landings in 1996, 642 (20%)[13] provided fishing cost information including the quantity used and price paid for fuel, bait, and ice and the total cost of

Table 1.—Estimated gross revenue of the Atlantic pelagic longline fleet in 1996.

Species	Number landed	Mean weight (kg dw[1])	Conversion factor (dw to rw[1])	Mean price ($/kg rw[1])	Gross revenue ($ U.S.)
Swordfish	72,096	35.1	1.33	6.60	22,213,340
BAYS[2] tunas					
Bigeye	16,865	31.5	1.25	7.69	5,105,879
Albacore	4,888	18.5	1.25	2.11	237,985
Yellowfin	65,636	32.0	1.25	4.42	11,592,138
Skipjack	506	5.4	1.25	3.49	11,916
Large coastal sharks					
Sandbar	20,976	14.4	1.39	0.69	289,234
Dusky	2,757	23.4	1.39	1.24	111,595
Silky	3,664	14.4	1.39	0.87	63,560
Bignose	24	19.4	1.39	1.53	990
Night	433	19.4	1.39	1.02	11,905
Blacktip	6,347	17.6	1.39	1.02	158,273
Spinner	822	19.4	1.39	1.11	24,565
Tiger	278	14.4	1.39	1.47	8,161
Hammerhead	3,791	28.4	1.39	0.22	33,198
White	32	19.4	1.39	1.42	1,224
Pelagic sharks					
Shortfin mako	3,124	48.6	1.39	1.91	403,318
Longfin mako	197	64.4	1.39	1.67	29,368
Porbeagle	1,059	31.5	1.39	1.80	83,463
Thresher	92	47.7	1.39	0.67	4,067
Bigeye thresher	495	44.1	1.39	2.82	85,635
Blue	207	32.0	1.39	0.16	1,430
Oceanic whitetip	331	15.8	1.39	0.18	1,288
Other	212	44.1	1.39	1.56	20,215
Other					
Greater amberjack	13	18.5	1.04	2.18	543
Banded rudderfish	6	19.4	1.04	1.69	204
Blackfin tuna	1,560	7.2	1.25	2.62	36,816
Bonito	109	2.7	1.00	1.89	556
Dolphin	37,671	30.2	1.20	3.93	5,360,885
King mackerel	100	19.4	1.04	3.69	7,424
Oilfish	5,599	9.9	1.00	1.33	73,907
Wahoo	3,678	12.2	1.04	3.98	184,868
Other tuna	242	31.1	1.25	5.91	55,521
Other shark	1,480	19.4	1.39	1.56	61,922
Other fish	1,751	19.4	1.04	1.73	61,078
Shark fins	46,321	20.3	0.05	25.93	1,220,759
Totals[3]	257,041				47,557,228

[1] dw = dressed weight, rw = round weight.
[2] BAYS represents the following tunas: bigeye, albacore, yellowfin, and skipjack.
[3] Landings exclude the number of shark fins.

groceries. A subset of trips also provided the number of light sticks used and price per stick. If this information was missing, the number of lights sticks used was obtained from the set forms and multiplied by the mean price per light stick. Similarly, if ice expenses were recorded on one trip, the average daily cost for that vessel was used for missing observations. A "miscellaneous" cost variable was also created for trips that included an estimate of the total cost of the trip that exceeded the sum of the itemized supply costs.[14]

Variable fishing costs also requires an estimate of labor costs, however, we could not use the reported payments due to the data problems discussed earlier. Instead, we use a share system (discussed in the following paragraph) to derive this expense.

According to an experienced NMFS observer (who would prefer to remain anonymous; Lee[15]), and following the approach used by McHugh and Murray[16], returns to vessel owners are

[13] The low response rate is attributed to first time collection of economic data, optional completion, and ambiguous phrasing of certain questions (Larkin et al., text Footnote 2).

[14] For the total trip cost, respondents were instructed to include the cost of the itemized fishing supplies, and "freight and handling" fees, and any additional expenses such as gear and vessel maintenance fees and replacement tackle.

typically calculated as a share of total revenues less trip expenses excluding groceries. The owner's share (60% if absentee, 50% plus a portion of the crew share if also the captain) is used to cover fixed costs including loan payments, dry dock charges, depreciation, and accounting fees. In this study, we assumed all trips hired a captain (i.e. the vessel owner received 60% of net revenues) to avoid including reimbursement for captain's labor in the return to the owner. This was necessary since the trip summary form did not ask whether the captain was the owner. Consequently, we assumed the labor costs to equal the captain and crew share (i.e. 40% of net revenues) less grocery expenses. The bulk of the analysis will focus on differences in net returns to the vessel owner to cover fixed costs appropriated to the trip (i.e. short-run returns).[17]

Results

Population vs. Sample Trip Characteristics

The Atlantic PLL fleet landed over 257,000 fish and sharks valued at nearly $48 million in 1996 (Table 1). Although over 30 species were landed, four accounted for 77% of the total number landed, namely: swordfish (28%), yellowfin tuna (26%), dolphin (15%), and sandbar sharks (8%). Collectively, these four species also accounted for nearly 84% of the total gross revenue.

The mean characteristics of the trip, set, and PLL vessel in 1996 are compared to the characteristics of the sample with economic data in Table 2. With the exception of the number of hooks between floats, the mean of the majority of characteristics are very similar (i.e. differed by less than 10%). In general, lower standard deviations were associated with the sample data.

The economic information contained in the sample data is summarized in Table 3. Estimated trip revenues averaged $13,313 to reported average costs

Table 2.—Comparison of total data set with economic subsample.

Variable	All PLL trips[1]	Sample PLL trips[1]
Number of trips	3,255	642
Number of sets	16,477	3,559
Number of vessels	272	125
Mean trip characteristics		
Number of sets	5.06 (3.87)	5.86 (3.64)[2]
Trip length (days)	10.50 (7.69)	11.79 (7.63)
Number landed		
Swordfish	22.23 (51.13)	20.63 (42.46)
BAYS tunas	26.99 (45.19)	27.03 (41.21)
Large coastal sharks	12.02 (85.23)	9.04 (27.10)
Pelagic sharks	1.76 (12.34)	1.22 (4.19)
Other	16.07 (38.37)	16.67 (36.27)
Mean set characteristics		
Hooks	631.6 (271.8)	615.3 (271.1)
Hooks between floats	8.37 (45.62)	18.72 (88.30)
Light sticks	277.1 (192.4)[2]	269.9 (218.56)
Length of mainline (km)[3]	40.72 (15.86)	37.29 (15.26)
Gangion length (fm)[3]	50.07 (67.29)	48.38 (52.01)
Floatline length (fm)[3]	32.53 (39.47)	34.58 (33.37)
Mean vessel characteristics		
Length (m)[3]	17.40 (4.28)	17.28 (4.20)
Displacement (net t)	60.27 (42.63)	63.16 (43.35)
Age (years)	14.73 (7.59)	14.27 (8.56)

[1] Parentheses contain standard deviations for mean values.
[2] Figure from trip logbook, which had fewer missing observations.
[3] One kilometer (km) = 0.62 miles, one fathom (fm) = 6 feet, and one meter (m) = 3.28 feet.

Table 3.—Sample trip characteristics (n = 642).

Variable	Mean	Standard dev.	Median
Number of crew[1]	3.56	1.43	4
Gross revenue			
Swordfish	$6,356	$13,083	$2,157
BAYS tunas	5,092	8,202	1,917
Large coastal sharks[2]	363	1,097	0
Pelagic sharks[2]	211	797	0
Other	1,291	3,133	306
Total[3]	13,313	16,619	8,916
Supply costs			
Fuel	1,373	1,519	1,031
Bait	1,437	1,463	960
Ice[4]	340	325	256
Light sticks[4]	687	863	360
Miscellaneous[4]	2,122	3,970	305
Total[3]	5,959	6,376	3,666
Net revenue[3]			
Total	7,354	13,494	3,736
Return to owner (60% of total)	4,412	8,097	2,242
Return to captain and crew (40% of total less groceries)	2,347	5,255	1,111

[1] Missing values not included in calculations.
[2] Revenues from the sale of shark fins accounted for 52% and 34% of total large coastal shark and pelagic shark revenues, respectively.
[3] Since the values for the "total" and "return" variables were calculated from the raw data, calculations based on the means or medians may be different.
[4] Missing values assumed to equal zero.

(i.e. variable costs excluding groceries and labor) of $5,959. The estimated owner's return (assuming a 60% share) averaged $4,412. The relatively large standard deviations suggests considerable variability in returns (more so than in the underlying revenues and costs), which indicates non-normal data distributions. For example, the standard deviations associated with gross revenues and costs exceeded the corresponding mean by 25% and 7%, respectively, but the standard deviation of the net return was 82% above the mean net return.

The median of the estimated owner returns equaled $2,242 (Table 3), indicating that returns were below that number on at least half of the trips in the sample. That the mean is 82% above the median indicates the distribution of returns, and, in fact, the distribution of each economic variable is positively skewed. Therefore, the median values are more representative of the fleet since they identify the characteristics of the majority better than the mean, which is sensitive to "outliers."[18] For example,

even though mean shark revenues were positive, only by examining the median value is it revealed that no sharks were landed on at least half the trips (i.e. the median is zero). Since the median revenue for each species group ranged from zero to 38% of the corresponding mean, the "average" trip landed considerably less than indicated by the mean. Overall, the median gross revenues and supply costs were 33% and 38%, respectively, below their corresponding means. Consequently, using mean revenues, costs, or net returns would significantly overestimate the economic benefits for at least half of the trips in the sample. More importantly, in terms of the implications for policy analysis, a zero median suggests that at least half the trips would not have been affected by regulations on large coastal or pelagic sharks.[19]

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[17] Using returns to cover fixed costs is appropriate for this trip-level (i.e. short-run) analysis. Fixed costs data would be needed, however, to construct an annual vessel profile. Unfortunately, such data have not been collected for this fleet.

[18] Using the empirical rule, 13% of the sample could be considered statistical outliers (Cavanos and Miller, 1993). These observations had either

unusually high costs relative to landings (e.g. costs included expenses for multiple trips or an unforeseen event ended the trip) or vice versa.

[19] Operations that did not land any sharks despite targeting those species could incur indirect costs resulting from certain regulations. For example, although trip limits would not have been constraining, the loss of option to participate in the fishery (i.e. loss of permit) would have.

Table 4.—Characteristics of sample trips by vessel length.

Variable	<13.95 m (45 ft)	13.95–19.72 m (46–64 ft)	19.73–26.09 m (65–86 ft)
Number of trips	192	234	216
Median characteristics			
Number of crew	2	3	5
Number of sets	3	6	7
Trip length (days)	5	11	15
Hooks per set	300	596	828
Length of mainline	20.9 km (13 mi.)	38.6 km (24 mi.)	48.3 km (30 mi.)
Vessel length	12.1 m (39.7 ft)	16.7 m (54.8 ft)	21.8 m (71.5 ft)
Median gross revenues			
Swordfish	$2,157	$1,232	$3,081
BAYS tunas	0	1,590	6,282
Large coastal sharks	48	0	0
Pelagic sharks	0	0	0
Other	91	378	474
Total[1]	4,168	9,506	12,831
Median supply costs			
Fuel	251	980	1,866
Bait	258	900	2,250
Ice	90	300	400
Light sticks	198	186	827
Miscellaneous	57	417	1,405
Total[1]	1,158	3,352	8,410
Net return to owner			
Median	1,771	3,187	2,643
Mean	3,763	4,668	4,713

[1] The sum of individual items equals the total for each trip, but the median may not.

Table 5.—Characteristics of sample trips by number of sets.

Variable	1–3 Sets	4–6 Sets	7–9 Sets	10–21 Sets
Number of trips	194	197	153	98
Median characteristics				
Number of crew	2	4	4	4
Number of sets	2	5	8	11
Trip length (days)	4	11	13	18
Hooks per set	492	700	700	700
Length of mainline (km)	22.5	41.9	45.1	43.8
Vessel length (m)	13.3	18.2	18.8	20.0
Median gross revenues				
Swordfish	$ 616	$ 1,849	$ 4,314	$ 9,089
BAYS tunas	0	2,296	4,794	8,242
Large coastal sharks	0	0	0	0
Pelagic sharks	0	0	0	0
Other	0	365	711	735
Total[1]	2,507	8,395	14,173	24,779
Median supply costs				
Fuel	219	1,095	1,294	2,406
Bait	258	960	1,500	2,685
Ice	96	280	300	386
Light sticks	99	560	667	1,597
Miscellaneous	43	526	1,009	1,591
Total[1]	981	3,588	5,950	9,902
Net return to owner				
Median	642	2,216	4,264	9,117
Mean	965	2,804	5,291	13,097

[1] The sum of individual items equals the total for each trip, but the median may not.

Trip Characteristics

By Subgroup

To improve the precision of fleet characterization, trip statistics are compared by vessel length, number of sets, quarter, region, and the percentage of revenues from swordfish in Tables 4 through 8, respectively. These variables were chosen because they represented both vessel characteristics and behavioral aspects of the fleet that can be (or have been) considered for use in FMPs (NMFS, 1999a; Cramer and Scott[1]). The distinctions between groups were based on frequency distributions of all PLL trips (Larkin et al.[2]), various NMFS documents, and expert opinion concerning the operation of the fishery from NMFS employees referenced in this paper and cooperative industry members.[20]

Vessel length ranged from 9.1 to 28.8 m (30–95 feet) in the fleet and

[20] Using a clustering procedure to choose variables and define groups was not employed since clustering by gross revenue, total trip expenses, and estimated owner returns produced groupings that were not conducive to policy analysis.

10.3 to 26.09 m (34–86 feet) in the sample such that mean vessel lengths in the fleet and sample were similar. Vessels were grouped into three categories (10.3–13.94 m, 13.95–19.72 m, 19.73–26.09 m). The sample trips were approximately equally distributed between groups. Examination of Table 4 indicates that on the typical trip taken by the longest PLL vessels, the trips were longer, used more hooks per set, and set longer mainlines. Comparison of median revenues reveals that longer vessels landed more swordfish and BAYS tunas (which is reflected in the higher revenues since price is constant) and incurred higher median costs per trip. Median returns to the vessel owner, however, were highest for midlength vessels due to relatively low costs. Median owner returns by vessel length ranged from 21% below to 42% above (for the shortest and the midlength vessels, respectively) the sample median of $2,242 (Table 3). Comparison with the corresponding mean returns reveals that using the mean (with trip frequency data) would produce a larger economic impact for an RIR analysis and would change the relative impacts experienced by vessels of different sizes.

In Table 5, trips are grouped into the following four categories: 1–3 sets, 4–6 sets, 7–9 sets, and 10–21 sets. The last group contains the fewest number of total trips (15% of sample) and does not contain trips reporting more than 21 sets (0.2% of the total) because none provided economic information. With the exception of the shortest trips (i.e. trips placing 1–3 sets), the hooks per set and vessel length associated with the typical trip were relatively robust to the number of sets placed or trip length. Despite the similarity of trips reporting from 4–21 sets, the median net returns to vessel owners ranged from $2,216 to $9,117 (1% below to 307% above the sample median). When less than 4 sets were placed only swordfish were landed on the typical trip and the median return to vessel owners was 71% below the sample median. Again, the mean returns exceed the median but both descriptive statistics provide the same ranking of net returns. Thus, for some stratifications, estimation of relative differences in net returns are robust to the use of either the mean or the median.

Seasonal differences in median returns were examined by quarter: January–March, April–June, July–September, and October–December. Compared

to previous groupings (by vessel length and sets), trips are relatively homogeneous across quarters in terms of trip and vessel characteristics (Table 6). Swordfish, BAYS tunas, and the "other" species were landed on the typical trip throughout the year. However, effort during the cooler months (October through March, the first and fourth quarters) was characterized by slightly longer vessels using longer mainlines. Median trip revenues were lowest from January through March, the same quarter with highest swordfish revenues. From April through June, when median trip revenues were highest, median revenues for other species were nearly three times that of the other quarters. Median trip costs were highest from October through December, primarily from increased fuel expenses. Overall estimated returns to the owner were highest in the second quarter and lowest in the first, ranging from $1,472 to $3,449 (34% below to 54% above the sample median). As with the disaggregation by vessel length, and as will be shown by regions, the descriptive statistic selected for analysis affects the absolute measure of net economic benefits and the relative ranking of benefits between subgroups.

Geographic differences are examined in Table 7 by the location of the offloading port, which correspond with the areas used in Cramer and Scott[1], namely: 1) Maine to Virginia, 2) North Carolina to Miami, 3) Texas to Key West, and 4) the Caribbean. The majority of trips in the sample offloaded at ports located from Texas to Key West where the typical trip was characterized by the longest vessels using the most hooks per set. The typical trip offloading in the Caribbean placed the most sets, used the longest mainline, and was at-sea for the most days. In general, the longest vessels and trips characterized the typical trip landing in the southern regions (Gulf of Mexico and the Caribbean). Median returns to the owner were highest in the Caribbean (258% above the aggregate sample) while median returns to trips landing in Gulf ports were lower than in the aggregate sample. The typical trip landing at a Gulf port reported the largest landings of other fish but the majority

of revenues were generated from BAYS tunas. Landings of BAYS tunas and pelagic sharks were largest from Maine to Virginia where lower costs resulted in higher median returns (19% above the aggregate median). The typical trip landing from North Carolina to Miami

reported the lowest returns. The Caribbean region, with the highest returns, is characterized by substantial median swordfish revenues relative to the total median revenue and the median revenues of other regions (median swordfish revenues of $22,184 in the Carib-

Table 6.—Characteristics of sample trips by quarter.

Variable	Jan.–Mar.	Apr.–June	July–Sept.	Oct.–Dec.
Number of trips	195	184	175	88
Median characteristics				
Number of crew	4	4	3	4
Number of sets	5	6	5	6
Trip length (days)	10	11	10	14
Hooks per set	667	700	600	554
Length of mainline (km)	41.9	38.3	32.2	45.1
Vessel length (m)	18.2	16.7	15.2	18.8
Median gross revenues				
Swordfish	$4,005	$2,003	$816	$3,697
BAYS tunas	883	2,561	3,179	2,128
Large coastal sharks	0	0	0	0
Pelagic sharks	0	0	0	0
Other	108	1,023	397	187
Total[1]	6,761	11,027	7,395	9,378
Median supply costs				
Fuel	988	1,058	780	1,417
Bait	1,079	1,035	712	1,037
Ice	225	262	260	300
Light sticks	560	421	132	631
Miscellaneous	471	363	190	87
Total[1]	4,188	3,861	2,817	5,309
Net return to owner				
Median	1,472	3,449	2,097	3,227
Mean	2,839	4,746	5,405	5,227

[1] The sum of individual items equals the total for each trip, but the median may not.

Table 7.—Characteristics of sample trips by region.

Variable	Maine to Virginia	N.C. to Miami, Fla.	Tex. to Key West, Fla.	Caribbean
Number of trips	86	189	319	47
Median characteristics				
Number of crew	3	2	4	4
Number of sets	5	4	6	8
Trip length (days)	8	7	12	17
Hooks per set	692	400	800	500
Length of mainline (km)	32.2	23.2	46.0	54.7
Vessel length (m)	15.6	13.3	19.7	16.4
Median gross revenues				
Swordfish	$ 462	$ 2,157	$ 1,849	$22,184
BAYS tunas	3,961	0	3,179	2,447
Large coastal sharks	0	0	0	0
Pelagic sharks	192	0	0	24
Other	91	183	412	227
Total[1]	7,060	4,826	9,387	26,227
Median supply costs				
Fuel	753	410	1,266	1,970
Bait	965	590	1,000	2,705
Ice	185	150	330	300
Light sticks	94	198	597	1,295
Miscellaneous	171	42	821	1,560
Total[1]	2,831	1,928	5,230	10,100
Net return to owner				
Median	2,671	1,740	2,022	8,020
Mean	6,672	3,679	3,099	12,188

[1] The sum of individual items equals the total for each trip, but the median may not.

Variable	Percentage of total revenues from swordfish			
	< 25%	25–49.9%	50–74.9%	75% +
Number of trips	272	105	87	178
Median characteristics				
Number of crew	4	4	3	3
Number of sets	5	6	7	4
Trip length (days)	11	13	12	9
Hooks per set	750	796	550	351
Length of mainline (km)	38.6	43.4	41.1	33.8
Vessel length (m)	18.2	20.9	16.7	14.6
Median gross revenues				
Swordfish	$0	$3,697	$5,854	$7,549
BAYS tunas	4,239	4,062	1,590	12
Large coastal sharks	0	0	0	0
Pelagic sharks	0	0	0	0
Other	470	435	412	93
Total[1]	8,332	9,082	9,748	8,828
Median supply costs				
Fuel	1,014	1,494	962	685
Bait	792	1,632	1,000	762
Ice	278	285	240	170
Light sticks	33	708	720	581
Miscellaneous	258	1,045	320	145
Total[1]	3,367	6,802	4,485	3,258
Net return to owner				
Median	2,017	1,885	2,419	3,288
Mean	3,834	2,830	4,351	6,260

[1] The sum of individual items equals the total for each trip, but the median may not.

bean region are nearly five times the combined median swordfish revenues of the other regions).

Note that the typical trip landing in the Gulf and Caribbean reported the same crew size and was characterized by longer vessels and mainline; however, swordfish landings and overall returns differed substantially. In this case, describing the fleet by length of the vessel or mainline would mask significant regional differences for the typical trip and thereby produce misleading economic effects of proposed spatial fishery closures.

Differences in median returns by swordfish targeting were also examined using the percentage of total revenue from swordfish since this species is often assumed to be the primary target of this fleet.[21] Table 8 shows that the typical trip characterized by swordfish revenues that accounted for at least 75% of total gross revenues

[21] The set forms ask for "target" and supply 9 species as options. This information could not be used to uniquely classify each observation by species since responses are not mutually exclusive (making the number of possible combinations prohibitive to compare) and the response rate was low (40% of sets, 22% of trips).

had the highest returns ($3,288), took shorter trips, placed fewer sets, used fewer hooks per set and a shorter mainline. When swordfish revenues comprised less than 50% of total revenues, the typical trip was taken by longer vessels that set more hooks and landed more BAYS tunas.

Comparing the aggregate median return to vessel owners' ($2,242, Table 3) with the median returns by subgroup ($642–$9,117, Tables 4 through 8) allows the identification of subgroups (i.e. trips with particular characteristics) that are most similar to the aggregate sample. These trips were taken by the longest vessels (20–26 m) that placed 4–6 sets during the third quarter (July through September) and landed at ports in the Gulf of Mexico or North Atlantic with swordfish revenues that accounted for 50–74.9% of the total; median returns ranged from 6% below to 18% above the aggregate median. Despite the similarity of some subgroups with the sample median, the median returns of the remaining subgroups differed more substantially (especially for trips placing a different number of sets or landing in a different region). Figure 1 compares the median

returns for the characteristics with the widest range.

To facilitate comparison of median returns with mean returns summarized in Larkin et al.[2], this information was included in Tables 4–8. For every subgroup the mean exceeded the median as anticipated due to the positively skewed distributions. This difference is important when absolute values are needed to estimate economic effects, such as in RIR and RFA analysis; however, relative differences in returns are only affected when the fleet is grouped by vessel length, season, and region. Hence, if the proposed regulation pertains to vessel size, seasons, and/or regions, the choice of descriptive statistic (mean vs. median) will likely affect the conclusions drawn from the analysis. Moreover, this effect could be significant given the observed variation in median net returns.

By Joint Subgroups

Given the dissimilarity in median owner returns between subgroups as shown in Figure 1, median returns were next calculated by the number of sets placed for each vessel length class, quarter, and region (i.e. the categories in Table 5 were disaggregated by the categories in Tables 4, 6, and 7, respectively) and compared to the aggregate median. As shown in Figure 2, median returns tended to increase with the number of sets across all groupings; however, within each set group returns varied quite substantially from the aggregate median by vessel length, quarter, and region. The median return was below the aggregate median for trips by the longest vessels placing the fewest sets, which could reflect trips that ended earlier than planned. The median return was highest for trips placing 10–21 sets that offloaded in the Caribbean. The typical trip in the Caribbean region also earned the highest returns in each set group. For trips placing the fewest sets (1–3), median returns were highest for short vessels and during the fourth quarter. For trips placing 4–9 sets, median returns were highest for mid-length vessels. Overall, median returns for these twice disaggregated groupings ranged from $1,498 to $18,241 per

trip or 168% below to 714% above the aggregate median.

In Figure 3, variations in median returns from the aggregate median are shown by the percentage contribution of swordfish to total trip revenues for each vessel length class, quarter, and region (i.e. the categories in Table 8 are disaggregated by those in Tables 4, 6, and 7, respectively). These differences reveal that targeting behavior had the largest impact on median regional returns. Swordfish targeted trips (where swordfish revenues were at least 75% of the total) in the northern region (Maine to Virginia) earned median returns in excess of 700% of the aggregate median. Conversely, Caribbean trips with swordfish revenues accounting for less than 25% of the total revenue also earned significantly higher median returns (nearly 600% above the aggregate median). When the medium and long vessels targeted swordfish, median returns were approximately 170% above the median, much higher than the median return earned by short vessels or for nonswordfish targeted trips. For comparison, recall that the examination of median returns by target level alone (Table 8) revealed that returns ranged from only 16% below to 47% above the aggregate median, which is a substantially narrower range than shown in Figure 3.

The temporal and spatial differences in median returns illustrated in the figures were based on revenues estimated using constant fish weights and prices from Table 1. Increasing precision in revenue estimation by including temporal and spatial price differences (as well as price difference by size of fish) would be an obvious extension to the present analysis. Of the 480 species, quarters, and regions for which data was possible (four quarters and four regions for each of the 30 species), landings were only reported for 263 (55%). Of the 263 prices needed to correspond with landings, only 95 (36%) were available from the NMFS database. In addition, only 27% of the prices needed for swordfish, yellowfin tuna, dolphin, and bigeye tuna (species that comprised over 93% of total revenues) were available. More importantly, prices were missing for 95%
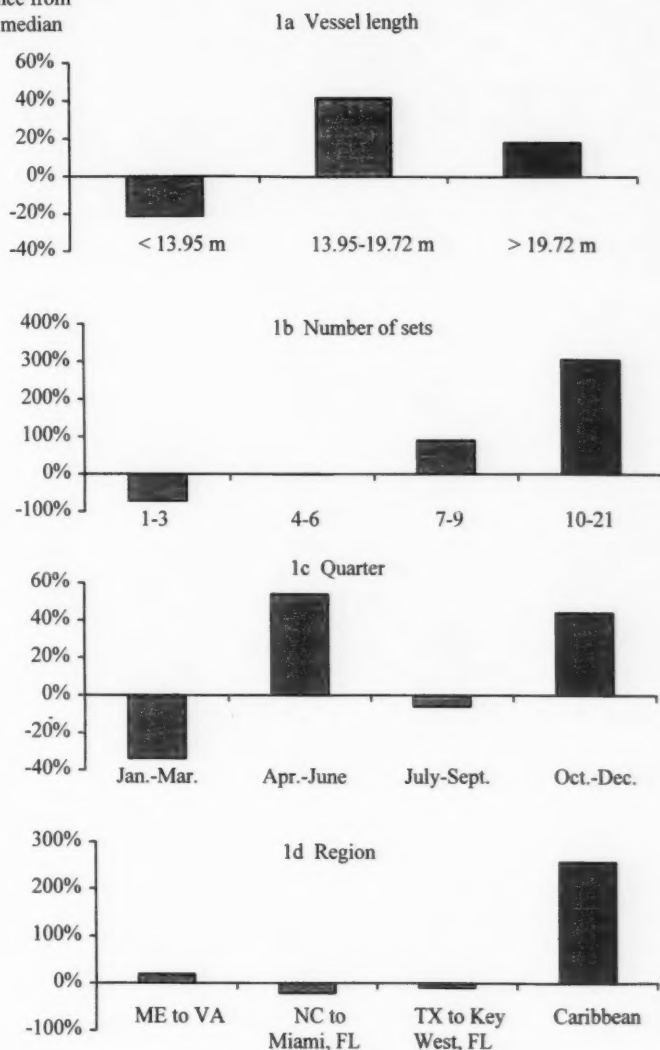

Figure 1.—Comparison of median net returns by trip type.

of yellowfin tuna landings and more than 98% of swordfish landings. Without temporal and spatial price information on (at least) the most predominate and valuable species, we could not adequately incorporate price heterogeneity. Temporal and spatial differences in landed weights may also impact the degree of heterogeneity in the fleet. A complete set of distinct weights that would correspond with the land-

ings (263 in total) was not available because it is not collected and, thus, could not be included. For some species, such as swordfish, price per pound can vary with the size of the fish; however, no data describing this relationship were available for any of the species.

Summary and Conclusions

The detailed data description provided transparency in 1) the proce-

dures used to synthesize the set logbook data, trip logbook data, fish prices, fish weights, weight conversion factors, and vessel information and 2) the definition of PLL observations, gross revenues, supply costs, labor costs, and net returns to the vessel owner. This transparency allows for the duplication of the data set or the creation of consistent data sets over time. Consistency in the data used by NMFS biologists is currently being provided through data fil-tering programs that identify, for example, incorrect location codes and summary sets. This analysis revealed that similar programs could be developed for the economic data. For example, a program could flag observations where 1) implied fish weights (calculated from the reported pounds kept and number landed) fall outside of a reasonable range, 2) estimated gross revenues exceed total payments, and 3) the reported number of sets and set dates do not coincide with trip dates or the number of corresponding set forms.

In terms of data analysis, the population consisted of all Atlantic PLL trips in 1996 that were known to NMFS through the logbook program. The sample data set consisted of a subset of these trips where cost information was provided on the trip logbook form. The sample was representative of the population in terms of the range of vessel types and fishing behavior (Table 2). The use of the logbooks to collect information appears to be effective given the response rate and that 1) fishermen are already familiar with the form and submission procedures; 2) the availability of corresponding catch data and gear use can supplement and verify (i.e. cross-validate) reported information; 3) the data can be analyzed at the trip, set, or (especially if mandatory) the vessel and annual level; and 4) the information can be collected at a relatively low cost. Continually collecting this information would also allow for the estimation of economic models over time and reduce the probability of recall bias compared to periodic surveys. Having a time series of economic information that corresponds to landings also complements studies that have focused on estimating regulatory effects using changes in landings (e.g. Cramer and Scott[1]). Ideally, the variable cost information would be supplemented with fixed cost data collected on permit renewal forms (Curtis[22]), voluntary proprietary data from cooperative industry members (as used here to verify reported variable cost information), and periodic surveys in order to conduct a long-run analysis.

In terms of the economic results, comparisons were made with trip-level data using (primarily) median net returns to the vessel owner to cover fixed costs. Given the multi-species nature of HMS fisheries and PLL gear, all landings were included in the underlying gross revenue calculation. Trip-level analysis was selected since 1) many decisions that affect returns are made
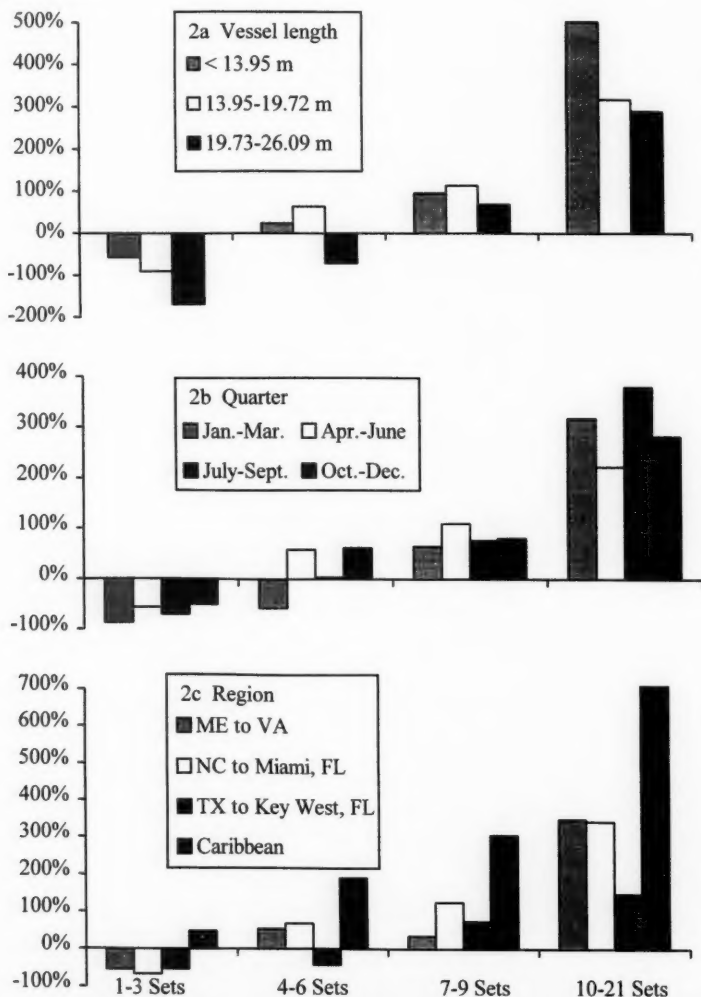

Difference from sample median

Figure 2.—Comparison of median net returns by number of sets.

[22]Curtis, R. 21 April 1999. Fisheries Statistics and Economics Division, NMFS, 1315 East-West Hwy, Silver Spring, MD 20910. Personal commun.

prior to the trip, 2) it has been considered the most complete level of production, and 3) NMFS has used this level for previous RIR and RFA analysis of this fleet.

The decision to focus on median statistics was determined by the skewed distributions of the variables and the NMFS statement (cited in the Introduction) that means may be misleading given the multi-species, multi-nature aspects of the PLL fleet. And, although the use of median values is not common in fisheries analysis, this particular descriptive statistic is applicable to fisheries for the same reasons it is used to compare housing prices and income. Additional benefits to using median values include the ability to identify the "average" or "typical" operation and that medians are robust to potential data "outliers" (e.g. trips with incomplete landing reports, aborted trips that show no landings but significant costs, or a small group of "highliners" that account for a relatively large share of landings). The focus on net returns to vessel owners to cover fixed costs was based on the data available and the NMFS recommendation that using gross returns or costs are less accurate. Lastly, the variables and variable levels used to define the subgroups in this analysis were based on those used by NMFS (i.e. species groups and regions), suggested by PLL vessel owners (i.e. number of sets), and considered important to industry members (i.e. season, vessel length, and swordfish targeting). Even so, these selections should not be considered the only or even the most appropriate variables to consider in future analysis. The selection of any particular variable(s) to analyze and, for that matter, descriptive statistic to use (mean and/or median) will depend on the proposed regulatory change and the analysis being conducted (RIR and/or RFA).

Using statistics from the aggregated data (Tables 2 and 3) implies that Atlantic PLL operations are homogeneous. These aggregate statistics may be useful in the broad context of Atlantic HMS species where the PLL fleet differs noticeably from other gear types; however, the variability in reported land-
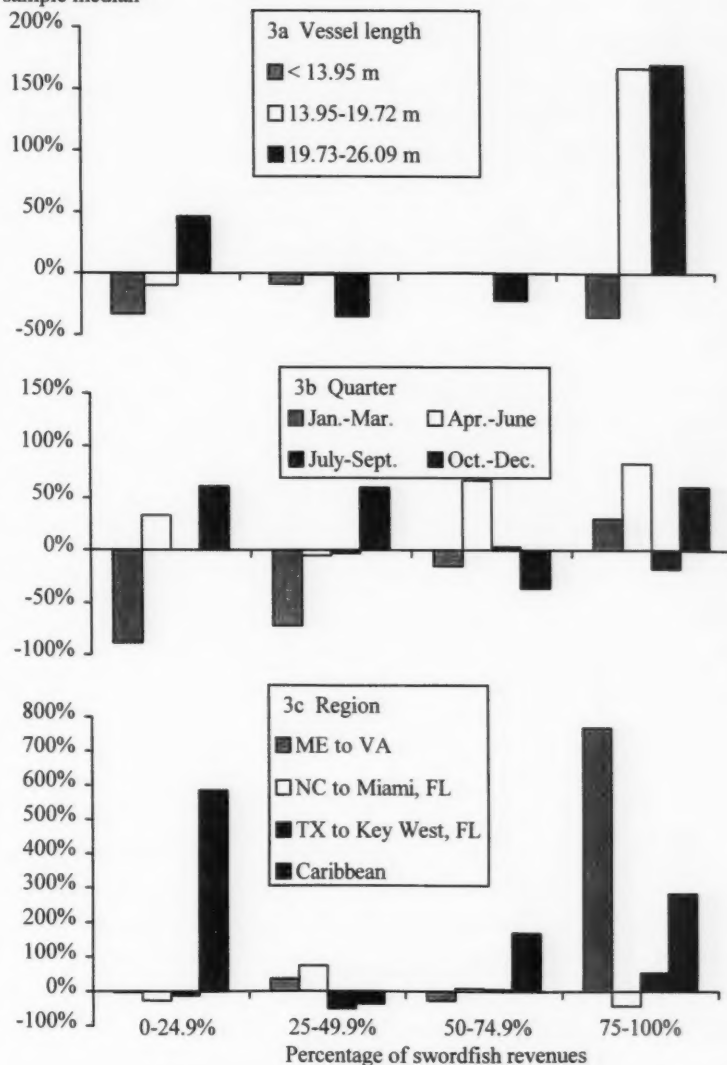

Figure 3.—Comparison of median net returns by swordfish revenues.

ings, set characteristics, vessel characteristics, and trip expenses (Tables 4–8, Fig. 1) suggests a significant degree of heterogeneity within the fleet. This heterogeneity was further evidenced by the finding that net economic returns, which vary with the composition of landings and trip costs, were dependent on vessel length, the number of sets

per trip (i.e. trip length), temporal and spatial fisheries participation, and the percentage of revenues from swordfish (Tables 4–8). Moreover, the differences in net returns were magnified when the vessel, trip, and behavioral characteristics were considered jointly (Fig. 2–3). Consequently, although the aggregate statistics may accurately reflect relative

differences in economic effects of proposed regulations between gear groups in Atlantic HMS fisheries, fleet heterogeneity may need to be considered in order to appropriately evaluate the economic effects (as required with the RIR and RFA) specific to the PLL gear group. Furthermore, with stratification into relatively homogeneous groups, the mean and median statistics will converge.

In summary, the aggregate mean net return exceeded the aggregate median by 97%. Thus, using the mean with trip frequency data to estimate fleetwide economic net benefits as allowed under an RIR could overestimate the economic effect. Given that median returns for different stratifications deviated by as much as 714% from the aggregate median return, using the stratified statistics would likely increase the estimated economic effect(s). In other words, using "different industry segments" (such as the stratifications posed in this paper) for an RFA analysis as is allowed, could produce results that differ substantially from results derived by assuming the aggregate economic information appropriately reflects the economic conditions faced by all PLL vessels. Moreover, the stratifications produced larger differences in median net returns from the aggregate median (Fig. 1) than if gross revenues were used. Thus, using gross revenues and thereby ignoring costs could underestimate the relative economic effects experienced by different industry sectors. Lastly, given the differences in median revenues by species under the stratifica-

tions (i.e. Table 3 vs. Tables 4–8) indicates that using revenues from a single-species would substantially change the analysis due to relative differences in the cost of landing the various species.

In conclusion, this paper provides a detailed summary of recently available data on the Atlantic PLL fishery. The results confirm the existence of heterogeneity within the Atlantic PLL fleet. Although the finding of heterogeneity within this fleet may not be a surprising result, and the selection of variables and subgroups are debatable, this analysis provides quantitative evidence of just how important these decisions (as well as the choice to use gross revenues or net returns) are to the estimation of economic effects of proposed regulatory changes that are likely to affect the Atlantic PLL fleet. This paper was not, however, intended to be all-inclusive of information needed, but rather to show how the available data can be used to improve and complement previous analyses. To assure that management decisions regarding the fate of the fleet and the future of the fishery are informed and efficient, continued effort in data collection and economic analysis is paramount.

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Effectiveness of a Rigid Grate for Excluding Pacific Halibut, *Hippoglossus stenolepis*, From Groundfish Trawl Catches

CRAIG S. ROSE and JOHN R. GAUVIN

Introduction

Diverse fishing gear modifications have been made and tested in efforts to alleviate bycatch problems in various fisheries. These include changes in the size and orientation of trawl meshes to avoid the catch of undersized fish (MacLennan, 1992), grates to release fish from trawls that target shrimp (Jones, 1993), and turtle excluder devices (TED's) to remove endangered sea turtles from shrimp trawls (Watson et al., 1986).

Pacific halibut, *Hippoglossus stenolepis*, may not be retained in any of the Alaska trawl fisheries, and halibut bycatch quotas are established for most of the groundfish trawl fisheries (Witherell and Pautzke, 1997). It is common for these fisheries to be closed because hal-

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ABSTRACT—A rigid grate was installed in a groundfish trawl to test its effectiveness in excluding Pacific halibut, Hippoglossus stenolepis, *from commercial flatfish catches in the Gulf of Alaska. The grate was located ahead of the trawl codend to direct halibut toward an escape opening while allowing target species to pass through toward the codend. In an experimental fishery, the escape rate of halibut was estimated at 94%, while 72% of the Dover sole,* Microstomas pacificus, *67% of the rex sole,* Glyptocephalus zachirus, *and 79% of the flathead sole,* Hippoglossoides elassodon, *were retained.*

ibut bycatch limits are reached and, as a result, substantial quantities of groundfish remain unharvested each year.

Flatfish fishermen have long been interested in developing gear modifications to reduce this bycatch and allow increases in fishing time and harvests. Some have developed their own designs for halibut excluders.[1] Most of these excluders put a size selection panel across the trawl a short distance ahead of the codend. Holes in the panel are large enough to allow smaller target species to pass but will exclude the much larger halibut, which are guided toward an escape slot. The performance of these excluders had not been scientifically evaluated. Although the ad hoc experience of these fishermen convinced some that these excluders were effective in particular fisheries, the need was seen for scientific evaluations of at least one excluder's selectivity. Costs associated with the intensive catch sampling and experimental design, which were necessary for such evaluations, were well beyond what any single fishing operation could reasonably manage during an open fishery.

In 1998, the Groundfish Forum, an organization representing groundfish trawl catcher/processors that fish in Alaska waters, obtained a National Marine Fisheries Service (NMFS) exempted fishing permit to test systematically the exclusion of halibut from flatfish trawls with a selected industry device. The work was done in cooperation with NMFS, which provided assis-

[1] Personal commun. with owners and captains of groundfish trawlers, including Mark Kandianis, Bob Hezel, Mark "Corky" Decker, Steve Spain, Scott Bryant, Mitch Hull, and Mike Peterson.

tance in the experimental design, fieldwork, and data analysis. The experiment was designed to determine if the excluder device could reduce halibut bycatch without significantly reducing catches of target species. Data analysis included estimation of the effects of the device on species and size compositions of the catch and to determine whether the device would be practical for use in Alaska groundfish fisheries.

Methods

The Alaska trawl industry participants were invited to submit designs of halibut excluders for effectiveness testing, together with information regarding their effectiveness. Four applications were received and reviewed by a panel of NMFS scientists. A rigid grate design submitted by the owners of the F/V *Legacy* was selected, based on criteria of expected effectiveness, considering any previous ad hoc experience or testing, and the suitability of the vessel and its fishing gear.

The outer frame of the F/V *Legacy*'s excluder grate was made of 6.4 cm (2.5 in) diameter tubular aluminum bent into a 1.8 m (6 ft) diameter circle, except that the top 38 cm (15 in) of the circle was removed and replaced with a straight section of tube (Fig. 1). Inside this frame, a grid of 15 cm × 15 cm (6 in × 6 in) square holes was formed by 5 cm × 0.64 cm (2 in × 0.25 in) vertical bars and 1.9 cm (0.75 in) diameter horizontal rods, welded together at all junctions. Short sections of PVC tubing were installed over each of the horizontal rods. Because these rollers protruded above the vertical bars, large fish could slide up the grate more easily. The grate was mounted in the interme-

diate section of the trawl (just ahead of the codend)(Fig. 2). This intermediate section consisted of a mesh tube made of four 36 mesh-wide, untapered panels of 14 cm (5.5 in) stretch mesh double polyethylene. Four riblines were installed at the corners where the panels joined and the grate was secured to each of these and laced to the mesh of the side and bottom panels. The attachment point on the top ribline was 71 cm (28 in, 5 meshes) aft of that on the lower riblines, creating a slope of about 28 degrees back from vertical.

Another panel of 14 cm (5.5 in) double mesh was attached to the top edge of the grate and along the top riblines, extending aft for 4 m (49 ft) where it was joined to the top panel of the intermediate. This panel and the top panel of the intermediate section formed a low tunnel through which escaping fish had to pass before exiting through a slit in the top panel.

An auxiliary grate, called the "deflector," was installed with a top-forward slant ahead of the main grate to direct fish downwards. The deflector grid had similar construction to the main grate but with 7.6 cm by 7.6 cm (3 in × 3 in) square openings. The back edge of the deflector and the main grate formed a 23 cm (9 in) wide slot through which fish had to pass to reach the escape tunnel. Sufficient flotation was installed on the top riblines to compensate for the weight of the grate and deflector.

Because the experimental design required more tows than one vessel could accomplish in the time available, an additional participant, the F/V *Alliance*, was picked at random from the remaining applications. Both vessels were catcher/processors which fish in the Gulf of Alaska for deep-water flatfish species, and both used low-opening commercial bottom trawls. The F/V *Alliance*, one of the smallest Gulf catcher processors (33 m in length), provided a means of determining whether this grate system could be fished effectively from a vessel with limited deck space.

The tests were conducted in the Gulf of Alaska deep-water flatfish fishery because halibut and deep-water flatfish species are concentrated in the same
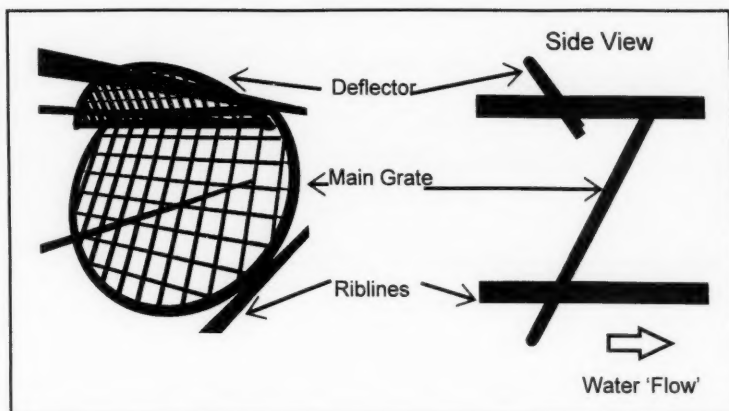

Figure 1.—Halibut excluder grate as installed in a trawl intermediate section. Mesh sides of intermediate are omitted for viewing, only riblines are represented.
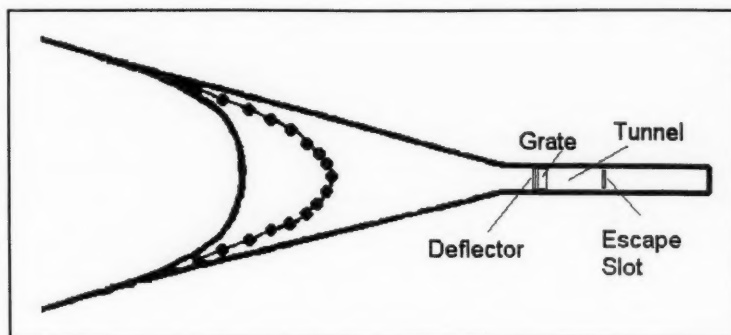

Figure 2.—Location of the excluder components in the trawl.

areas, and exclusion of halibut could dramatically increase harvest of those target species. Also, the halibut encountered by this fishery tend to be relatively large, making exclusion more effective. Target species include rex sole, *Glyptocephalus zachirus;* Dover sole, *Microstomus pacificus;* and flathead sole, *Hippoglossoides elassodon.* Arrowtooth flounder, *Atheresthes stomias,* are an abundant but low-value species that is also taken, but it is usually not targeted.

Vessels alternated experimental and control gears to create pairs of tows (blocks) conducted under similar conditions. Pairing of tows helped to eliminate variation in catches due to location, time, and vessel effects. The gear

used for the first tow of each block was randomly determined, and the vessel captain was not informed of the selection until after location and time of the tow had been decided. The second tow of each block was made on a parallel track, as close as practical in time and location to the first, matching speed and other towing parameters.

The F/V *Legacy* alternated tows with two matched nets: one with and one without the excluder. The excluder was exchanged between the nets at the midpoint of the experiment. The F/V *Alliance* used one net, exchanging intermediate sections with and without the excluder between experimental and control tows. Tow duration was allowed to vary within blocks to accommodate

for the loss of catch through the excluder. Analyses were done on catch per distance fished to prevent differences in tow lengths from introducing a bias.

Catch volumes were measured from full codends or from a bin into which the catch had been dumped. These were converted to weights using a conversion factor for deep-water flatfish of 0.95 metric tons per cubic meter (t/m^3), a value used by the NMFS Observer Program for this fishery.[2]

To improve survival of discarded halibut, as many as possible were sorted out of the catch as it was transferred into a holding bin. A NMFS trained and certified fisheries observer worked with the deck crew to count and measure all halibut and return them to the sea. To ensure that the rest of the catch was available for sampling, no fish were moved out of the bin into the factory until the deck sampling was completed and the observer went down to the factory. All halibut recovered in the factory were also counted and measured.

The catch was sampled to determine species composition by filling baskets from conveyor belts as the catch passed from the holding tank to the factory. These samples, totaling at least 300 kg, were accumulated from several collections taken systematically throughout the emptying of the bin.

Bridge personnel recorded the position and time of the start and end of each tow. They also recorded the type of tow (experimental or control), depth, and towing speed.

A recording temperature-depth-light level sensor was attached to the trawls. Tow length was the distance traveled between the time the trawl depth stabilized at the beginning of the tow until the winches were started during retrieval.

To allow tests for proportional differences with additive statistical tests, a (natural) logarithmic transformation was applied to all catch rates. This also helped to normalize the catch rate distributions. The parameter which was used as a measure of the effect of the excluder (E_{EX}) was the difference between the

[2] Sarah Gaichas, NMFS Alaska Fisheries Science Center, Seattle, Wash. Personal commun.

Table 1.—Operational and environmental averages of two vessels participating in tests of a halibut excluder.

Vessel	Speed (knots)	Distance fished (n.mi.)	Catch rate (t/n.mi.)	Depth (m)	Light level (microE/m² – s)	Temperature (°C)
F/V Alliance	2.5	6.3	0.34	226	9×10^{-7}	6.0
F/V Legacy	3.1	4.1	1.22	217	5×10^{-7}	5.8

transformed catch rate from each tow with the excluder (subscript e) and the comparable rate from the control tow (subscript c) in the same block (pair):

$$E_{EX} = Ln\left(\frac{Catch_e}{Distance_e}\right) - Ln\left(\frac{Catch_c}{Distance_c}\right). \quad (1)$$

This parameter was calculated for each block for each major species in the catch. The antilogs (exponential) of the means and confidence intervals of E_{EX} estimates were used to provide estimates of the proportion retained when the excluder was used. The E_{EX} values were analyzed with t-tests to determine whether the excluder significantly changed catch rates. Halibut size selectivity was analyzed using a similar procedure.

Results

The experiment to test the excluder was conducted from 18 to 28 September 1998. The F/V Legacy completed 31 blocks, and the F/V Alliance completed 30. The crews of both vessels developed effective procedures for setting, retrieving, changing, and storing the selection grate. The F/V Alliance demonstrated that this rigid grate system could be used on a vessel with a small deck and an aft net reel. They were able to complete these tows in the alloted time, even with the experimental requirement of approximately 15 changes between configurations with and without the grate.

Both vessels started towing west of Kayak Island in the central Gulf of Alaska (Fig. 3). After completing five blocks, the F/V Legacy moved to the northern and western edges of Portlock Bank where it completed the rest of its tows. The F/V Alliance remained near Kayak Island for the duration of the experiment. Most tows were made between 200 and 250 m depth, with a few blocks by both vessels in the 100–200 m range, and a few by the F/V Legacy were made between 250 and 325 m.

Flathead sole made up less than 1% of all catches on Portlock Bank, so those blocks were excluded from the analysis for that species. In addition, there were two blocks where both Dover sole and rex sole made up less than 1% of the catches in both control and experimental tows. Those blocks were excluded from the analysis for those species, because the experiment explicitly sought to measure the performance of the excluder in the deep-water flatfish fishery.

The F/V Legacy towed for shorter distances and at higher speed than the F/V Alliance and achieved higher average catch rates (Table 1). Average depth, light level, and temperature were similar for the two vessels.

With the data from both vessels combined, the excluder retained only 6% of the halibut while keeping 62% of the aggregated deep-water flatfish species (Fig. 4). The retention rates for the individual deep-water flatfish species varied from 48% for arrowtooth flounder to 79% for flathead sole. Dover and rex sole retention rates were 72% and 67%, respectively. All of these values, except that for flathead sole, were significantly different from the null hypothesis of no effect at the p< 0.01 level with a Bonferroni adjustment for multiple tests.

The retention rates were significantly different between the vessels only for rex sole (p<0.03) and halibut (p<0.001) (Fig. 5). For both species, the F/V Legacy allowed more fish to escape than the F/V Alliance. This was also the direction of the nonsignificant differences for the other species.

Because the length of each captured halibut was measured, the size composition and selectivity data were abundant for that species. Fish in the 5–10 kg (75–93 cm length) size class made up 45% of the weight of halibut caught in the control net. The grate excluded all but 2% of the halibut weight in this and larger size classes (Fig. 6). The only size class of halibut passing through the grate
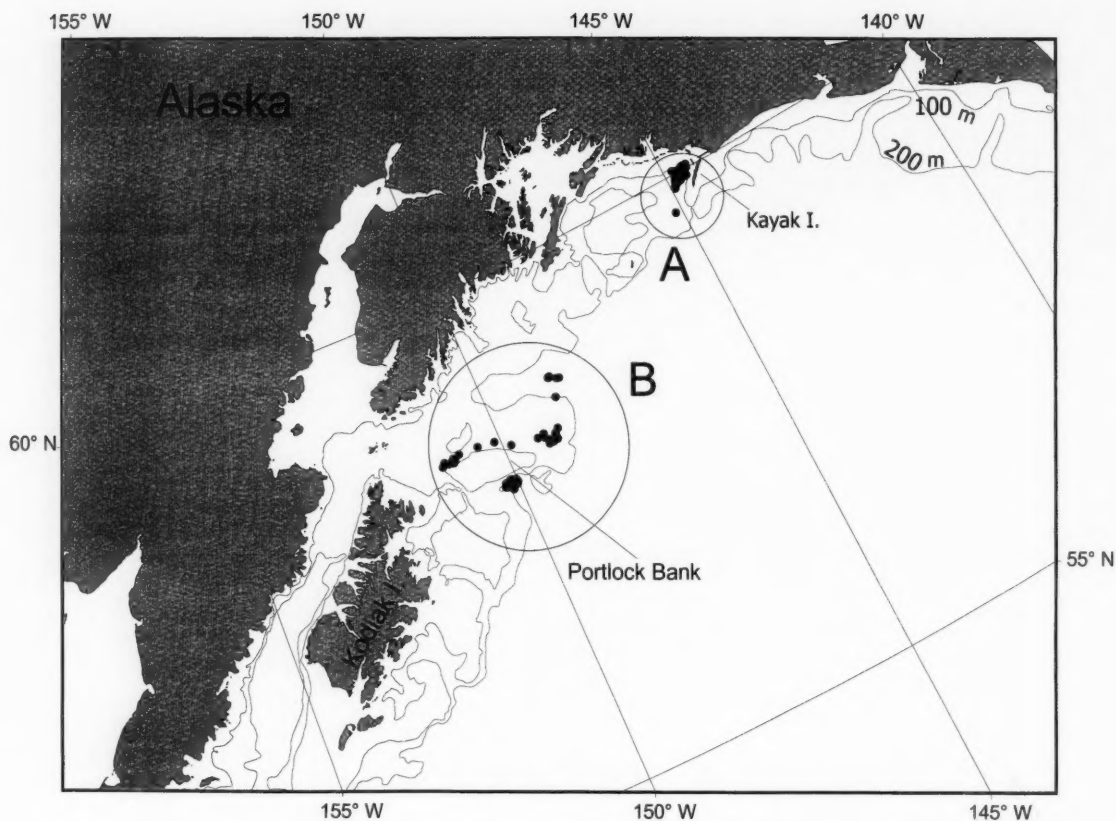
Figure 3.—Locations of experimental trawl tows. Area A—All Alliance blocks and Legacy blocks 1–5, Area B—Legacy blocks 6–31.
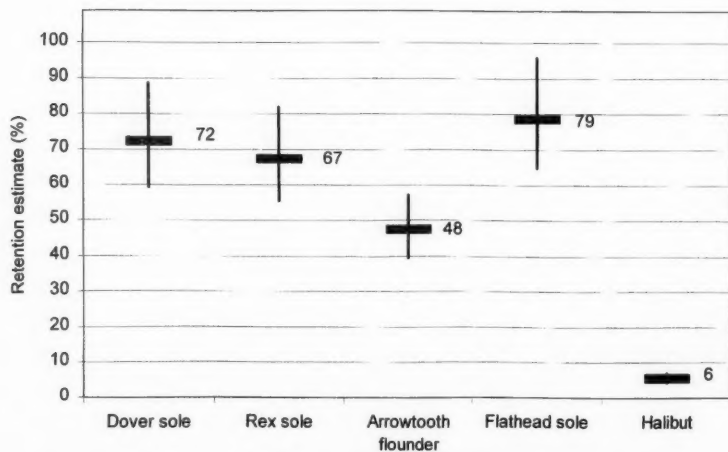

Figure 4.—Percent (mean and 95% confidence intervals) of deep-water flatfish species retained by a trawl equipped with a halibut excluder when compared with catches from a trawl of the same design without the excluder.

in large proportions included fish weighing less than 3 kg (64 cm), of which 46% (by weight) was retained. The retention difference between size classes was statistically significant ($p<0.0001$). While some size composition samples were collected for the target species, these were insufficient to effectively analyze size selectivity.

A problem recognized early in the field work was that some debris and fish would remain ahead of the grate when the trawl was retrieved. This was particularly true of large skates (Rajidae). To allow some assessment of whether an accumulation in front of the grate was affecting its sorting ability, the weight of fish ahead of the grate was estimated for each F/V *Legacy* experimental tow. This weight varied from 0 to 0.9 t with an average of 0.3 t. Linear regres-

sions of each species' retention percentage with this weight showed no useful relationship for any species. The best correlation was for rex sole where the regression explained only 10% of the variation.

Summary and Conclusions

The experiment demonstrated that the halibut excluder grate system dramatically reduced the catch of halibut. However, there were also moderate reductions in catches of rex sole, Dover sole, and flathead sole. The halibut exclusion was size selective, with 46% of the halibut weighing less than 3 kg retained, while nearly all of the halibut larger than 5 kg escaped. The size sampling of the target species was insufficient to detect selectivity differences by size groups. As a result, questions regarding the escapement of larger flatfish were not resolved. Both vessels developed procedures for handling their nets, with the excluder installed, in ways that did not significantly impede normal fishing operations. This was particularly important for the F/V *Alliance*, which had restricted deck space and only a single aft net reel.

The deep-water flatfish fishery has been prevented from catching a large proportion of its allowable catches in the past, because halibut bycatch limits have led to closures each year since the halibut caps have been in place. Reductions in halibut bycatch rates by using excluders would thus present an opportunity to harvest a greater percentage of the target flatfish quotas. However, decreases in catch rates of target species when using the excluder were important and could affect the economic viability of the fishery. Fishermen may not be able to justify the operating costs of fishing if revenue per day is too low due to the reduction of catch rates of target species. Uncertainty regarding size selectivity leaves the possibility that a more severe loss of larger, more valuable, rex sole would further reduce catch values.

While the grate excluder system was effective in reducing halibut bycatch, some avenues are open for further improvement. A way to prevent the accumulation of large fish, particularly
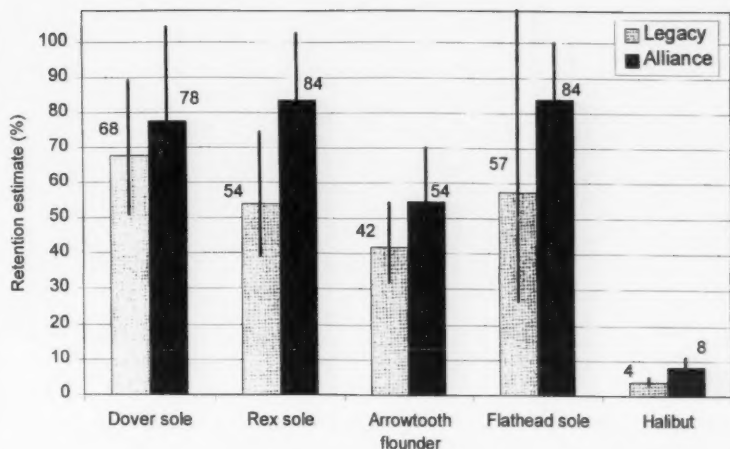
Figure 5.—Comparison between vessels of the percent (mean and 95% confidence intervals) of deep-water flatfish species retained by a trawl equipped with a halibut excluder when compared with catches from a trawl of the same design without the excluder.
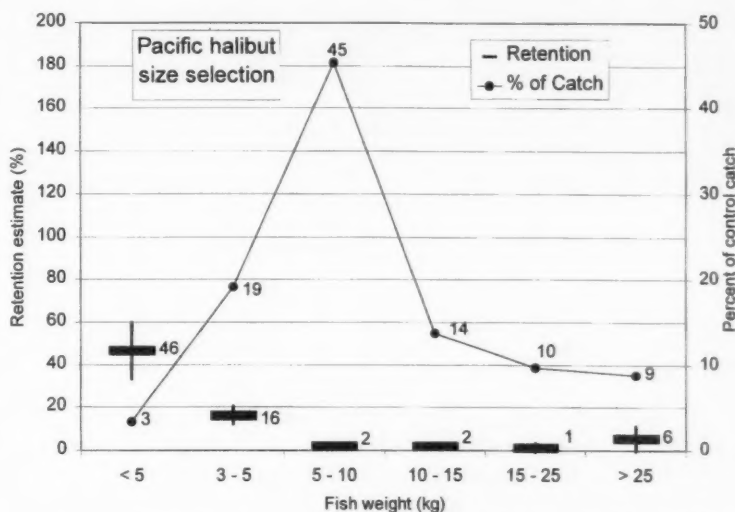
Figure 6.—Comparison between size classes of the percent (mean and 95% confidence intervals) of halibut retained by a trawl equipped with a halibut excluder when compared with catches from a trawl of the same design without the excluder.

skates, and debris ahead of the grate would likely improve the effectiveness of the device. Procedures should be sought to improve the retention of target species, especially larger individuals. Even if this causes some additional retention of halibut, it would provide a greater range of choices with which to achieve management and fishery goals.

Even though the F/V *Alliance* was able to use the rigid grate efficiently, it may be worthwhile to explore excluders that are more easily handled on smaller vessels. In this regard, mesh excluders have been tried by several vessels and, though they were not selected for this study, their further testing and development are warranted.

Acknowledgments

The authors gratefully acknowledge the contributions of the Kodiak Fish Company, vessel skippers Scott Bryant and Clint Walker, and the crews of the F/V *Alliance* and F/V *Legacy* in developing and providing the excluder and carrying out the experimental fishing. Thanks are also due to John Henderscheit and the four observers who played key roles in the field and initial data processing work, Greg Krivonak, Bonnie Gautier, Sergio Henrici, and Greg Wells. Gary Stauffer and Sue Salveson were instumental in the process of developing and obtaining the permit. It is also important to recognize that the development of halibut excluders has been mutually pursued by a number of individuals in the Alaska fleet. Their cooperation has been vital to the development of this useful tool.

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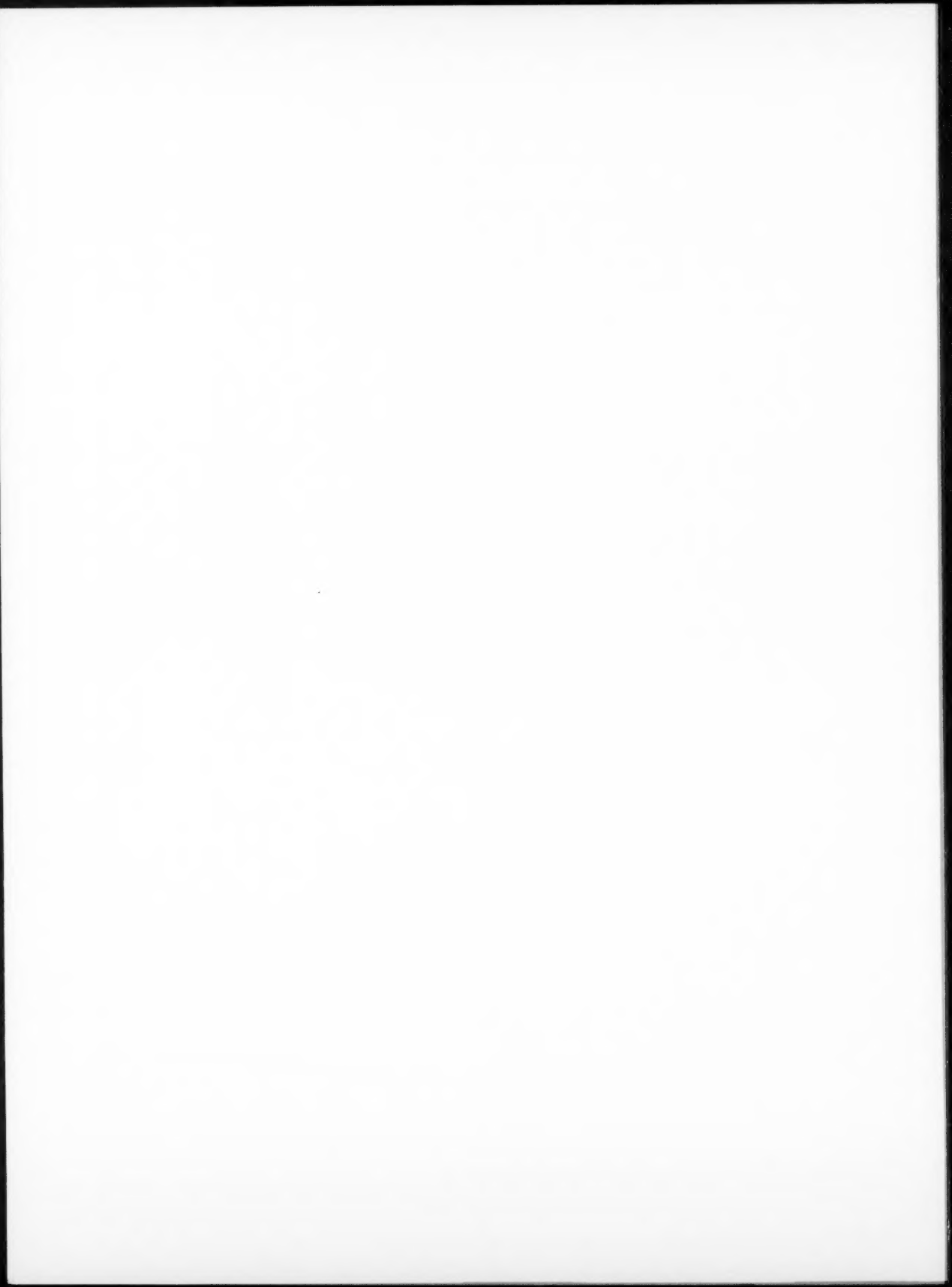
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